OSTEOLOGY AND CLASSIFICATION OF THE NEOTROPICAL CHARACOID FISHES OF THE FAMILIES HEMIODONTIDAE (INCLUDING ANODONTINAE) AND PARODONTIDAE

TYSON R. ROBERTS[1]

CONTENTS

Introduction 412
Osteological observations 415
  Terminology 415
  Material examined 415
  Hemiodontidae 416
    Hemiodontinae 416
      Cranium 416
      Otoliths 416
      Facial bones 417
      Jaws and jaw teeth 417
      Suspensorium 417
      Hyoid and branchial arches 417
      Weberian apparatus 418
      Pectoral girdle 418
      Pelvic girdle 418
      Vertebral counts 418
      Caudal skeleton 418
    Bivibranchiinae 418
      Cranium 418
      Otoliths 418
      Facial bones 418
      Jaws 419
      Jaw teeth 419
      Suspensorium 419
      Hyoid arch 420
      Gill arches 420
      Gill rakers 420
      Pharyngeal teeth 421
      Weberian apparatus 421
      Pectoral girdle 421
      Pelvic girdle 422
      Vertebral counts 422
      Caudal skeleton 422
    Anodontinae 422
      Cranium 422
      Otoliths 422
      Facial bones 422
      Jaws 423
      Suspensorium 423
      Hyoid and branchial arches 423
      Gill rakers 423
      Weberian apparatus 424
      Pectoral girdle 424
      Pelvic girdle 424
      Vertebral counts 424
      Caudal skeleton 424
  Parodontidae 424
      Cranium 424
      Otoliths 425
      Facial bones 425
      Jaws and jaw teeth 425
      Suspensorium 426
      Hyoid and branchial arches 426
      Weberian apparatus 427
      Pectoral girdle 427
      Pelvic girdle 427
      Vertebral counts 427
      Caudal skeleton 427
Discussion 427
  Relationship between Hemiodontidae and Parodontidae 427
  Transfer of Anodontinae from Curimatidae to Hemiodontidae 429
  Remarks on lower taxa 432
    Genera of Hemiodontinae 432
    Genera of Bivibranchiinae 432
    Genera and species of Anodontinae 433
    Genera of Parodontidae 433
Conclusion 434
Literature cited 434
Figures 437

Abstract. The family Parodontidae is highly specialized and readily distinguished from Hemiodontidae and all other characoid families. The three genera it contains differ relatively little from each other and clearly cannot be separated at a

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[1] Museum of Comparative Zoology, Cambridge, Massachusetts, U. S. A. 02138.

level higher than that of genus. In contrast, the seven genera of Hemiodontidae fall into four subfamilies, each characterized by specialized trophic structures unlike those of any other characoids. The osteology of Parodontidae and of three hemiodontid subfamilies is described and figured, based on study of all genera except *Atomaster* and *Pterohemiodus*. Although similarities in the jaws and suspensoria are suggestive of shared specializations, the evidence that the two families are closely related is inconclusive. The genera and species of Hemiodontinae are still poorly defined and need systematic study. The trophic structures of *Bivibranchia*, considered as a whole, are more specialized than those of any other characoid. Although *Argonectes* is much more primitive than *Bivibranchia*, its specializations clearly indicate that it belongs in Bivibranchiinae. Bivibranchiinae are the only characoids with protrusible jaws, and the mechanism of protrusion is unique. The subfamily Anodontinae, which is transferred into Hemiodontidae from Curimatidae, consists of a single genus with probably only two valid species, *Anodus elongatus* and *A. melanopogon*.

The genera and subfamilies of the two families can be classified as follows

- Parodontidae
  - *Parodon, Apareiodon, Saccodon* (*Parodontops* a synonym of *Saccodon*)
- Hemiodontidae
  - Hemiodontinae
    - *Hemiodus* (*Hemiodopsis* a synonym), *Pterohemiodus* (of doubtful validity)
  - Bivibranchiinae
    - *Argonectes, Bivibranchia, Atomaster* (probably a synonym of *Bivibranchia*)
  - Micromischodontinae
    - *Micromischodus*
  - Anodontinae
    - *Anodus* (*Eigenmannina* a synonym)

INTRODUCTION

The poorly known characoid families Hemiodontidae and Parodontidae include some of the most interesting fishes in the fresh waters of South America. Hemiodontidae range throughout the lowlands of the Guianas and the basins of the Orinoco and Amazon, and southwards to include the Plata basin. Mostly six inches to a foot long when adult, they form small schools in lakes and large rivers. All are swift swimmers with streamlined bodies. Seven genera and about 27 species are currently recognized, belonging to four subfamilies: Hemiodontinae, Bivibranchiinae, Anodontinae, and Micromischodontinae. The best known genera are *Hemiodus* Müller 1842, *Bivibranchia* Eigenmann 1912, and *Anodus* Spix 1829 (*in* Agassiz and Spix, 1829). *Bivibranchia* and its poorly known relatives *Argonectes* Böhlke and Myers 1956 and *Atomaster* Eigenmann and Myers 1927 are the only characoids with truly protrusible upper jaws. The greatly reduced premaxillaries are freed from the cranium, and the maxillaries and anterior end of the suspensorium are very loosely bound to it. When the lower jaw is depressed, the entire upper jaw and the palatine-ectopterygoid portion of the suspensorium move slightly forward and strongly downward and away from the cranium. The mouth is apparently able to close when the upper jaw is protruded. The highly specialized mechanism of protrusion is probably unlike that in any other teleosts. *Anodus*, hitherto assigned to Curimatidae, is one of the few Amazonian fishes with pharyngeal structures apparently specialized for filter feeding on plankton (Roberts, 1972: 138–40). It has edentulous jaws and far more gill rakers than any other characoid. The gill arches are exceptionally elongate, and the number of gillrakers undergoes a considerable increase with growth of individuals.

Parodontidae occur in the eastern half of Panamá, on the Pacific and Caribbean coasts of Colombia and the Pacific coast of Ecuador, in the Orinoco and Amazon basins, in the Guianas, and southwards to include the Plata basin. There are about 25 species, mostly four to six inches long when adult. All are mountain stream fishes, typically found in swift streams at altitudes from 100 to over 1000 meters. Several species occur in headwaters on the periphery of the Amazon basin, but no specimens have been reported from the Middle or Lower Amazon. Their expanded and flattened pectoral fins are presumably adapted to help maintain position in swift current. Nuptial tubercles occur in several species (Wiley and Collette, 1970). The pedicellate teeth and the apparently very mobile (but nonprotrusible) premaxillaries are highly specialized for browsing on algae. Three genera are currently recognized: *Parodon* Valenciennes 1849 (*in* Cuvier and Valenciennes, 1849), *Saccodon* Kner and Steindachner 1863, and *Apareiodon* Eigenmann 1916. *Saccodon,* restricted to coastal basins in Panamá, Colombia, and Ecuador, is of exceptional interest to evolutionary biologists because populations of the two principal species exhibit extraordinary polymorphism with respect to trophic structures (Roberts, 1974). Greater diversity of premaxillary tooth morphology occurs in a single population of *Saccodon dariensis* than in all species of *Parodon* and *Apareiodon* combined.

The pedicellate, multicuspid dentition in the nonprotrusible upper jaw of *Hemiodus* is very similar to that in many Parodontidae, and parodontids with relatively terminal mouths such as *Saccodon terminalis* (cf. Roberts, 1974) and some species of *Apareiodon* bear a striking resemblance to *Hemiodus.* Most students of characoids, including Regan (1911), Eigenmann (1912), Fowler (1950), Géry (1959), and Greenwood et al. (1966), either stated that Hemiodontidae and Parodontidae are closely related or else at least provisionally accepted this hypothesis by placing them either in the same family or subfamily or next to each other in a classification.

The scant literature on the osteology of Hemiodontidae and Parodontidae can be rapidly reviewed. Regan (1911) gave an extremely brief account of the jaws and suspensorium of Hemiodontidae and Parodontidae. Travassos (1951; 1952) gave extensively illustrated accounts of the opercular series, jaws and dentition of Parodontidae. The highly specialized replacement tooth trenches characteristic of the family can be seen in many of his figures. Géry (1959) briefly compared the superficial skull bones of Parodontidae and Hemiodontidae. Géry (1963a) described the jaws and suspensorium of *Bivibranchia;* unfortunately, there are several errors in this account. Lastly there is my account of the osteology of *Micromischodus* (Roberts, 1971), a new genus from the rio Negro and Middle Amazon. These six references constitute all that has been published on the osteology of the two families.

The present account deals with the osteology of Parodontidae and of the hemiodontid subfamilies Hemiodontinae, Bivibranchiinae and Anodontinae. The osteology of the one remaining hemiodontid subfamily, the monotypic Micromischodontinae, has already been treated (Roberts, 1971), but may be reviewed briefly here. *Micromischodus* is the only hemiodontid in which the lower jaws bear teeth throughout life. In all others the lower jaw is either toothless throughout life or becomes toothless early in life. The specialized unicuspid pedicellate dentition on the jaws and pharyngeal toothplates of *Micromischodus* is unique. My original account should have mentioned that *Micromischodus,* like other hemiodontids, has three openings into each posttemporal fossa. Excepting the teeth and elongated slender pharyngeal toothplates, the osteology of *Micromischodus* is very similar to that of *Hemiodus.*

Following the general osteological accounts, diagnoses are presented for all of the higher taxa: Hemiodontidae, Hemiodontinae, Bivibranchiinae, Anodontinae, and Parodontidae. The possible relationship of Hemiodontidae and Parodontidae to each other is reviewed in the Discussion section. The question of relationships of Parodontidae and Hemiodontidae to other characoids is left in abeyance, pending osteological and morphological investigations of other groups including Chilodontidae and Anostomidae. I have already pointed out that the relationship of the "semifunctional" preformed replacement teeth to the functional unicuspid pedicellate teeth on the pharyngeal toothplates of *Micromischodus* may parallel an evolutionary stage on the way to the multicuspid pharyngeal teeth characteristic of Chilodontidae and Anostomidae (Roberts, 1971). The most important conclusion about classification of characoids reached in this paper is that Anodontinae belong to Hemiodontidae rather than to Curimatidae.

The biology of Hemiodontidae and Parodontidae is largely unknown. Knöppel (1972) gave an account of the stomach contents of several species of Parodontidae and Hemiodontidae (Hemiodontinae and Bivibranchiinae). His findings may be summarized as follows: Parodontidae and Hemiodontinae ingested mainly sand, detritus, algae (diatoms mentioned for *Parodon*, filamentous algae for *Hemiodus*), and higher plants. Of the ten species of Hemiodontinae examined, only *Hemiodus immaculatus* had fed on chironomid larvae. The stomach contents of this species also included ephemeropteran larvae but no plant material of any kind. In three species of *Bivibranchia* Knöppel found sand, detritus, and chironomid larvae. One of the species also contained algae (kind not specified) and a copepod (Harpacticidae?). Stomach contents of *Micromischodus* (Roberts, 1971: 8) include an assortment of bottom material or detritus, some of which may be droppings of other fishes, and many small insects, especially larval Diptera and a corixid. There is no published information on the food items of *Argonectes* and *Anodus*. The behavior and reproductive biology of Parodontidae and Hemiodontidae have not been studied.

TABLE 1. AMOUNT OF TROPHIC SPECIALIZATION AMONG VARIOUS CHARACOID TAXA.

	Brycon	Curimatidae	*Hemiodus*	*Anodus*	Serrasalminae	*Micromischodus*	Parodontidae	Cynodontidae	*Argonectes*	Prochilodontidae	*Bivibranchia*
Jaws	1	1	1	1	1	1	2	2	2	2	2
Jaw teeth	1	1	2	1	2	2	2	2	2	2	2
Replacement teeth	1	0	1	0	1	1	2	1	1	2	1
Lips	0	0	0	0	0	0	0	0	0	2	0
Palate	0	0	0	0	2	0	0	0	0	0	2
Suspensorium	0	0	0	0	0	0	1	1	2	1	2
Pharyngeal arches	0	0	0	2	0	1	0	1	1	0	2
Gill rakers	0	1	1	2	0	0	1	1	1	1	1
Pharyngeal teeth	0	0	0	0	0	2	0	0	0	1	2
Pharyngeal epithelium	0	1–2	0	0	0	0	0	0	0	2	2
TOTAL	3	4–5	5	6	6	7	8	8	9	13	16

This paper provides further documentation for the hypothesis that diversification of feeding structures has played a major role in the evolution of higher taxa in the suborder Characoidei (Roberts, 1967; 1971; 1973). An attempt to compare the amount of trophic specialization among various characoids seems worthwhile. Regardless of whether the conical tooth morphology and the arrangement of the teeth in *Salminus* are correctly interpreted as primitive (Roberts, 1969), the feeding structures of this genus are clearly generalized for characoids. Using *Salminus* as a guideline, I have judged the character states of ten structures involved in the mechanics of feeding as they occur in a variety of characoid taxa. The structures are scored either "0" (generalized condition), "1" (some specialization), or "2" (high specialization). The individual scores for the ten structures are then totalled to give the amount of trophic specialization in each taxon. Subjectivity is probably inevitable in any methods that could be devised to determine the amount of specialization between organisms as unalike as the proverbial apples and oranges, and it has not been eliminated here. The method has been arbitrarily designed, and evaluation of the character states is still relatively subjective. On the other hand, the steps have been broken down, so that they can be followed by other workers, subjected to reevaluation and further analysis, extended to additional taxa, and perhaps improved upon. The data for a number of taxa is presented in Table 1. Note that the range of theoretically possible total scores is from 0 to 20. *Salminus,* generalized in all respects, would automatically score 0. Of the groups tabulated, *Bivibranchia* is most specialized, with a score of 16. I do not know of any other characoid group that would score this high. The group with the next most specialized feeding structures is probably the Prochilodontidae, which scores 13 (see Roberts, 1973, for an account of the feeding structures of this iliophytophagous family). *Argonectes,* which shares several trophic specializations with *Bivibranchia,* scores only 9. The piscivorous family Cynodontidae also scores 9. Most piscivorous groups, including the Serrasalminae (piranhas), score low, mainly because they tend to have generalized pharyngeal trophic structures. The iliophagous Curimatidae are generalized in most features and score very low. Of groups not tabulated, Anostomidae and Chilodontidae have perhaps the most specialized feeding structures and would probably score around 8 or 10.

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OSTEOLOGICAL OBSERVATIONS

Terminology

The osteological terminology used in this account is based primarily on that in Weitzman (1962), with three main exceptions, namely that for gill arches, precaudal and caudal vertebrae, and caudal skeleton. The gill arch terminology followed is that recommended by Nelson (1969). It is essential to define gill arch elements precisely and to standardize their terminology if the information they represent is to be useful in phyletic analysis. Nelson emphasized the distinction between endoskeletal elements and dermal toothplates, an important clarification. An adequate nomenclature for the bony elements collectively known as basihyals and basibranchials has yet to be developed. In characoids these apparently include dermal as well as endoskeletal elements, and yet the dermal elements in most cases are not toothplates. In many characoids the basihyal is a compound element, consisting of an anterior (dermal?) portion and a posterior endoskeletal portion. Concerning the vertebrae, caudal vertebrae are herein defined as the first vertebra bearing a complete hemal canal and all of the vertebrae succeeding it, counting the compound ural centrum as one. The precaudal count includes the four vertebrae bearing the Weberian apparatus. The terminology for the caudal skeleton is that proposed by Monod (1969).

Material Examined

This account is based on alizarin preparations of the following specimens of Hemiodontidae and Parodontidae (MCZ = Museum of Comparative Zoology, Harvard; MZUSP = Museu de Zoologia da Universidade de São Paulo; CAS = California Academy of Sciences; USNM = Smithsonian Institution; FMNH = Field Museum of Natural History, Chicago):

Anodus elongatus, MCZ 20671. One specimen, 180 mm. Lago Alexo, Amazonas, Brazil. Thayer expedition.

Anodus melanopogon, MZUSP 5959. Three specimens, 54.0 to 55.0 mm. Mouth of the rio Purus, Amazonas, Brazil. Expedição Permanente da Amazônia, 1–5 April 1967.

Apareiodon affinis, FMNH 71228. Three specimens, 26.5 to 46.8 mm. Río Uruguay at Soriana, south of Dolores. C. C. Sanborn, 25–31 January 1927.

Apareiodon itapicuruensis, FMNH 56991. Two specimens, 19.8 and 21.0 mm. Rio Itapicuru at Queimadas, Bahia, Brazil. J. D. Haseman, 2 March 1908.

Argonectes longiceps, MCZ 20635. One specimen, 198 mm. Rio Xingu, Amazonas, Brazil. Thayer Expedition.

Bivibranchia protractila, CAS(SU) 48847. One specimen, 39.9 mm. Río Cassiquiare at mouth of Río Curamoni, Venezuela. C. Ternetz, 7 March 1925; CAS(SU) 48608. One specimen, 115.2 mm. Rio Negro at Camanaos rapids, Brazil. C. Ternetz, 23 January 1925.

Hemiodus quadrimaculatus, MCZ 29926. One specimen, 35.0 mm. Lower Potaro River at Tumatumari, Guyana. C. H. Eigenmann, 1908.

Hemiodus semitaeniatus, MCZ 49072. Two specimens, 54.4 and 55.8 mm. Jauré ranch, North Savannah, Rupununi, Guyana. C. Hopkins, 18 May 1971.

Parodon caliensis, MCZ 47682. One specimen, 63.5 mm. Probable locality data: small streams of Sierra Azul, easternmost range of Andes [Peru?]. O. Barton, December 1945.

Parodon guyanensis, MCZ 48969. One paratype, 38.5 mm. Upper Mana River at Saut-Fini, French Guiana. Lelong, 25 November 1957.

Saccodon dariensis (Meek and Hildebrand), USNM 208503. Two specimens of dental morph I, 83.4 and 89.4 mm, and two specimens of dental morph IV, 97.2 and 100.7 mm. Río Sabalo, Bayano basin, one mile above Naragandi, Panamá. Battelle Memorial Institute NW Lab., 21 March 1967.

Saccodon wagneri Kner and Steindachner, MCZ 48745. Four specimens of dental morph I, 45.5 to 57.2 mm; and MCZ 48746. Five specimens of dental morph IV, 52.0 to 103.3 mm. Arroyo Bambine (tributary of Río Cristal), Guayas basin, at Montalvo. T. R. Roberts, R. Gilbert, F. Silva M., 6 November 1971.

The only genera not represented in this list are the hemiodontids *Pterohemiodus* Fowler 1940 (closely related to, and perhaps indistinguishable from, *Hemiodus*), and *Atomaster* (a close relative and possible congener of *Bivibranchia*). Alizarin preparations of the following Curimatidae have been examined: *Acuticurimata macrops, Cruxentina nasa, Curimata cyprinoides, Curimatorbis ocellatus, Gasterotomus latior, Potamorhina pristigaster, Semitapicis planirostris,* and *Suprasinelichthys laticeps.*

Hemiodontidae

HEMIODONTINAE

Cranium (Figures 1–5). Frontoparietal fontanel complete; frontal portion narrow anteriorly, widening in front of epiphyseal bar; parietal portion uniformly wide. Ethmoid narrow, its head with a dorsomedian projection and lateral projections (one on either side) articulating with premaxillaries. Supraoccipital crest flattened dorsally; tip of supraoccipital spine rounded in dorsal view, extending to end of cranium. Posttemporal fossae well developed, with three openings. Lateral opening, largest in size, bordered entirely by epiotic and pterotic; dorsomedial opening, bordered by epiotic, parietal and supraoccipital; ventroposterior opening, lying in posteromedian portion of epiotic. Lateral and dorsomedial openings separated from each other only by a narrow bony bridge formed by epiotic. Dilator groove well developed, frontal participating in its formation.

Vomer with a concave lamellar component ventrally and two separately formed lamellar components dorsolaterally. Lateral ethmoid large, with anterior processes articulating with vomer. Rhinosphenoid present. Interorbital septum large, rhinosphenoid and orbitosphenoid widely separated from parasphenoid. Posterior portion of parasphenoid cleft for most of its length. Subtemporal fossa well developed.

Otoliths. Otoliths of generalized characoid morphology, similar in size and shape to those in *Brycon* (cf. fig. 7 in Weitzman, 1962).

Facial bones (*Figure 6*). Facial bones present no unusual features. Circumorbital series complete, with a supraorbital, antorbital, and six moderately large infraorbital bones bearing infraorbital canal of cephalic laterosensory system. Infraorbital canal with posteriorly directed branches on infraorbital bones 3 and 4. Infraorbital bones flat, ventral portions of infraorbitals 1–4 not strongly curving beneath head. Infraorbital 1 not greatly enlarged. Size and shape of infraorbitals as in *Micromischodus:* infraorbital 3 largest, infraorbital 2 relatively slender. Infraorbital six contacting or closely approaching supraorbital.

Opercular bones of generalized characoid morphology, apparently without conditions of phyletic significance at familial or generic levels. Lateral surface of opercle smooth. Dorsoanterior corner of opercle strongly notched.

Jaws and jaw teeth (*Figures 6–10*). Premaxillary, with a short ascending process, loosely joined to maxillary; maxillary larger than premaxillary, its proximal end with a median knoblike projection. In *H. semitaeniatus* descending limb of premaxillary lies medial to anterior edge of maxillary; in *H. quadrimaculatus* descending limb of premaxillary much shorter, scarcely or not at all extending medially to maxillary. Upper jaw with a single row of 10–15 or more loosely articulated (movably attached) multicuspid teeth. Tooth crown rounded, cusps in a straight row, number of cusps increasing with age. In *H. semitaeniatus* a maximum of two replacement teeth for each functional tooth; in *H. quadrimaculatus* up to four replacement teeth per functional tooth. Inner surface of premaxillaries without bony partitions separating rows of replacement teeth. In *H. semitaeniatus* about eight teeth articulated with premaxillary and seven with maxillary; in *H. quadrimaculatus* about four or five teeth with premaxillary and five with maxillary. In *H. quadrimaculatus* premaxillary curving around replacement tooth rows more strongly than in *H. semitaeniatus.*

Lower jaw toothless, elongate. Portion of dentaries meeting at symphysis slender; middle portion of dentary moderately elevated. A single fenestra near anterior edge of dentary. Coronomeckelian bone low set, lying well below dorsal margin of articular bone.

Suspensorium (*Figures 6–8, 11*). Palatine straight, immovably attached to ectopterygoid, its anterior end moderately expanded. Ectopterygoid loosely (movably) attached to quadrate. Mesopterygoid loosely attached to quadrate and metapterygoid; metapterygoid loosely attached to hyomandibular. Anterior margin of metapterygoid separated by a gap from dorsoposterior margin of quadrate. Metapterygoid-quadrate fenestra relatively small. Anteroventral limb of metapterygoid (entering border of metapterygoid-quadrate fenestra) developed more strongly and anterior margin of hyomandibular more oblique in *H. quadrimaculatus* than in *H. semitaeniatus* (compare Figs. 7 and 8).

Hyoid and branchial arches (*Figures 12–14*). Hyoid arch without unusual features, of generalized characoid morphology. Four or five branchiostegal rays (four in *H. semitaeniatus,* five in *H. quadrimaculatus*). Proximal portion of next to last branchiostegal ray not enlarged (cf. *Argonectes* and *Micromischodus*). Basihyal slender, consisting of two ossifications, an anterior (dermal) bone and a posterior (endoskeletal) bone. Urohyal fairly long, its lateral wings moderately depressed and its dorsomedian lamina moderately high and extending slightly posterior to lateral wings.

Branchial arches including ceratobranchial 5 of relatively generalized characoid morphology, endoskeletal elements excepting infrapharyngobranchials and basibranchials similar in size and shape to those in *Brycon.* Three basibranchials; basibranchial 1 minute, basibranchials 2 and 3 very long. Three infrapharyngobranchials infrapharyngobranchials 2 and 3 greatly enlarged.

Gill rakers variable in form, often with large ctenii (not true teeth) (Fig. 14), and relatively numerous: 45 gill rakers on first gill arch of a 35.0-mm *H. quadrimaculatus,* 58 in a 55.8-mm *H. semitaeniatus* (Fig. 13), 70 in a 235-mm *H. microlepis* and 75 in a 113.5-mm *H. notatus.*

Pharyngeal dentition consisting of numerous small conical teeth, either nonpedicellate or with very short pedicels, confined to three or four pairs of upper pharyngeal toothplates and a single pair of lower pharyngeal toothplates. Upper pharyngeal toothplates on ventral surface of infrapharyngobranchials 2 and 3 and loosely associated with median ends of epibranchials 3 and 4.

Weberian apparatus (*Figure 15*). Weberian apparatus, very similar to that of *Micromischodus* and *Brycon meeki,* apparently without features of phyletic significance at generic or familial levels.

Pectoral girdle (*Figure 16*). Pectoral girdle of generalized characoid morphology, apparently lacking in features of phyletic significance at generic or even family levels. Three postcleithra, postcleithrum 3 slender for most of its length but with a lamellar portion near its proximal end (as in *Micromischodus, Brycon dentex* and many other characoids).

Pelvic girdle (*Figure 17*). Pelvic bone simple anteriorly; ischiac process relatively large. Four radials associated with each pelvic bone; innermost radial commashaped. Pelvic fin with 11 rays. Pelvic girdle evidently without features useful for phyletic analysis at generic or family levels.

Vertebral counts. Total vertebral and precaudal plus caudal vertebral counts in two specimens of *H. semitaeniatus* 40 (26 + 14) and 41 (26 + 15).

Caudal skeleton (*Figure 18*). Caudal skeleton with two or three epurals and two uroneurals. Hypurals 3–6 separate. Hypural 2 fused to hypural 1 and not to complex ural centrum. No bony projections comparable to parhypurapophyses or hypurapophyses. Principal caudal rays 10 + 9.

BIVIBRANCHIINAE

Cranium (*Figures 19–24*). Cranium of *Argonectes* similar in most respects to that in Hemiodontinae and Micromischodontinae. Anterior end of ethmoid of distinctive shape: narrow, slightly up-turned, with a dorsomedian groove terminating as a notch in tip of ethmoid (Fig. 19). Shapes of frontoparietal fontanel and of three openings into each posttemporal fossa as in *Hemiodus* and *Micromischodus.* Pterotic spine pronounced, epiotic spine moderate. Dilator fossa well developed. Rhinosphenoid moderately large and relatively simple in shape (Fig. 20). Posterior portion of parasphenoid cleft for virtually its entire length. Subtemporal fossa well developed. Hyomandibular fossa formed by contiguous surfaces of sphenotic and pterotic (Fig. 21).

Cranium of *Bivibranchia* broadly similar to that of *Argonectes* but with some notable departures: anterior end of ethmoid depressed, without a dorsomedian groove but with anterolateral projections; vomer relatively broad; rhinosphenoid greatly enlarged and of distinctive shape (Fig. 23); pterotic and epiotic spines enlarged; anterior portion of parasphenoid immediately in front of attachment of gill arches with a strong, ventrally projecting keel (absent in *Argonectes*). Dilator fossa less prominent than in *Argonectes.* Condition of frontoparietal fontanel, openings into posttemporal fossae, and hyomandibular fossa similar to *Argonectes.* In *Argonectes* and *Bivibranchia* ventromedian opening into posttemporal fossa partially closed by thin irregular bridges of bone from epiotic.

Otoliths. Otoliths of Bivibranchiinae not examined.

Facial bones (*Figures 25–29*). In *Argonectes* facial bones departing only in minor details of size and shape from those of *Hemiodus*: infraorbitals 1 and 4 relatively small. Infraorbital 6 contacting supraorbital.

In *Bivibranchia* facial bones differ in size and shape from those in *Argonectes* and *Hemiodus*: infraorbital 2 enlarged; infraorbital 1 relatively elongate; infraorbital 6 widely separated from supraorbital. Dorsal margin of opercle straight, without indentation characteristic of other hemiodontids.

Jaws (*Figures 25, 27–29*). Lower jaw similar in shape to that of Hemiodontinae; *Argonectes* and *Bivibranchia* differ from *Hemiodus* in having a posteriorly directed knob on symphyseal process of dentary and coronomeckelian bone elevated in position. In *Bivibranchia* coronomeckelian more elevated than in *Argonectes,* forming part of dorsal margin of lower jaw (Fig. 28); articular bone more elongate in *Bivibranchia,* its anterior end loosely fitted into dentary (not directly applied to internal surface of dentary), its posterior end with a knoblike projection that fits into a recess in median surface of quadrate when lower jaw is depressed.

Upper jaw highly specialized. Premaxillary minute. Maxillary slender and highly curved, more so in *Bivibranchia* than in *Argonectes.*

Jaw teeth (*Figures 27–29*). Jaw teeth highly specialized, diagnostic of subfamily. A single row of eight or nine minute, tricuspid, pedicellate teeth loosely attached to premaxillary and concave proximal portion of maxillary. Three or four preformed replacement teeth for each functional tooth in *Argonectes,* one or two in *Bivibranchia.* Lower jaw edentulous.

Suspensorium (*Figures 27–28*). In *Argonectes,* palatine, mesopterygoid and hyomandibular relatively generalized in morphology, not greatly different from these bones in other characoids. Mesopterygoid contacting and movably articulated with ectopterygoid and metapterygoid, not contacting palatine or quadrate. Ectopterygoid, quadrate and metapterygoid highly specialized: proximal end of ectopterygoid with a slender rounded head loosely fitting into a deep recess or socket in anterior margin of quadrate just above quadrato-mandibular joint. Metapterygoid movably articulated with mesopterygoid and hyomandibular, as in *Hemiodus.* Metapterygoid-quadrate joint more extensive (and less movable?) than in *Hemiodus,* metapterygoid quadrate foramen relatively small. Ventroposterior edge of metapterygoid contacting dorsal margin of symplectic distal end.

In *Bivibranchia* every bone in suspensorium highly specialized in shape and in relationships to other bones. Palatine bone S-shaped, its anterior end slender, forming a concavity into which elongated distal end of maxillary rides. Proximal end of ectopterygoid slender, forming the finger of a highly specialized, loose-fitting "finger and ring" joint with quadrate bone. Anterior margin of quadrate dorsal to quadrato-mandibular joint with a completely open ring of bone inside of which rides proximal end of ectopterygoid. Median surface of quadrate ventral to quadrato-mandibular joint with a well-developed concavity into which free-ending posterior projection from articular bone slides when lower jaw is depressed. Ectopterygoid of a highly modified and characteristic shape, much more specialized than in *Argonectes.* Ectopterygoid terminating anteriorly in a slender process to which ectopterygoid-vomerine ligament attaches. Ectopterygoid with an extensive movable articulation with quadrate, contact with metapterygoid reduced compared to *Argonectes,* no direct contact with ectopterygoid. Metapterygoid-quadrate articulation even more extensive than in *Argonectes,* rectilinear. Metapterygoid-quadrate foramen reduced in size, as in *Argonectes,* but metapterygoid and distal end of symplectic separated by a distinct gap. Metapterygoid-hyomandibular articulation specialized; hyomandibular with a strutlike process immovably joined to dorsoposterior margin of metapterygoid. Metapterygoid strengthened by a well-developed longitudinal keel on its median surface extending anterior to and immediately below strut from hyomandibular.

Hyoid arch (*Figures 30, 34–36*). In *Argonectes* basihyal slender and moderately elongate, composed of separate anterior and posterior ossifications firmly sutured together; anterior ossification about twice as long as posterior one. Dorsal and ventral hypohyals closely joined. Hyoid bar perhaps slightly shorter than in *Hemiodus* but otherwise not strongly modified. Five branchiostegal rays, four on ceratohyal and one on epihyal. Proximal portion of branchiostegal ray 4 expanded so that it reaches dorsal edge of ceratohyal, as in *Micromischodus*. Urohyal moderately long, its lateral wings relatively narrow and only slightly depressed (ventral surface of urohyal moderately concave). Dorsomedian lamina moderately high, extending to posterior end of urohyal. Head of urohyal (attaching to ventral surface of ventral hypohyals) moderately wide, "neck" immediately behind head narrowed.

In *Bivibranchia* basihyal slender and moderately elongate, composed of separate anterior and posterior ossifications; anterior ossification about one-third as long as posterior one, and firmly attached to anterior end of posterior ossification, but not sutured to it as in *Argonectes*. Dorsal and ventral hypohyals closely joined. Hyoid bar slightly shorter than in *Hemiodus*, expanded dorsally and ventrally at junction of ceratohyal and epihyal; edge of dorsal expansion sharp; middle of hyoid bar thickened. Five branchiostegal rays, four on ceratohyal and one on epihyal. Branchiostegal ray 4 with its proximal portion only slightly enlarged. Urohyal specialized, its lateral wings wider and more depressed than in *Argonectes*, dorsomedian lamina forming a strong low-lying ridge behind head of urohyal but increasingly weak on posterior half of urohyal until it is almost absent. Head and neck of urohyal wider than in *Argonectes*.

Note. In *Argonectes* branchiostegal membranes relatively free from isthmus, gill openings extending forward almost to point of attachment of branchiostegal rays to hyoid bar. In *Bivibranchia* branchiostegal membranes broadly joined to isthmus below middle of eye, gill openings extending forward only to posterior ends of branchiostegal rays 1 and 2.

Gill arches (*Figures 31–37*). In *Argonectes* gill arches relatively generalized for characoids, similar to those in *Hemiodus*, without any obvious specializations. Apparently three basibranchials; basibranchial 1 minute. Small accessory ossifications (dermal bones?) between basibranchials 1 and 2 and basibranchials 2 and 3. Three hypobranchials. Four infrapharyngobranchials (a separate ossification dorsal to posteriormost upper pharyngeal toothplates interpreted as infrapharyngobranchial 4). Epibranchials 1–3 and ceratobranchials 1–4 morphologically generalized, their adpharyngeal surfaces simply rounded (as in *Hemiodus*). Epibranchial 4 with a moderately large abpharyngeal laminar extension (a widespread feature in characoids).

In *Bivibranchia* gill arches highly specialized. Three basibranchials; basibranchial 1 much larger than in *Argonectes* and most other hemiodontids, almost as long as basibranchials 2 and 3. Three hypobranchials. Hypobranchial 1 specialized: elongate and enlarged, peculiarly bowed inwards, its anterior end distinctly expanded. Hypobranchial 2 less modified than hypobranchial 1, but also relatively elongate. Three epibranchials. Epibranchials 1–3 and ceratobranchials 1–4 highly specialized, their adpharyngeal surfaces with a greatly expanded, thin bony lamina. These laminae completely separate gill rakers on leading edge of each gill arch from those on trailing edge, and are covered by highly specialized epithelium.

Gill rakers (*Figures 34, 36*). In *Argonectes* gill rakers present on leading and trailing edges of gill arches 1–4 and on leading edge of gill arch 5 (ceratobranchial 5). A 177-mm specimen has $14 + 1 + 8$ rakers on arch 1, $8 + 1 + 9$ on arch 2, $8 + 1 + 9$ on arch 3, 7 + 1 + 6 on arch 4, and 8 on arch 5.

In *Bivibranchia* gill rakers present on leading and trailing edges of most of gill arches 1–4 and on leading edge of arch 5. Gill rakers absent on basibranchials, infrapharyngobranchials, hypobranchials 1 and 2, and anterior half of ceratobranchial 1. Gill rakers slender and moderately elongate, only tripodlike basal portion and sometimes a small part of shaft absorbing alizarin. A 39.9-mm specimen has 12 + 1 + 11 rakers on arch 1, 12 + 1 + 15 on arch 2, 13 + 1 + 17 on arch 3, 10 + 1 + 17 on arch 4, and 23 on arch 5. A 115.2-mm specimen has 12 + 1 + 10 on arch 1, 14 + 1 + 17 on arch 2, 10 + 1 + 19 on arch 3, 12 + 20 on arch 4, and 23 on arch 5. (Note: in smallest rakers basal portion ossifies in two places; cf. rakers on epibranchials 3 and 4 in Fig. 36).

Remarks. In *Bivibranchia* the adpharyngeal epithelium is thrown into a uniform series of prominent, finely papillose ridges. One such ridge extends from the base of each gill raker on the leading edge of the gill arches to the base of the gill raker at the same position on the trailing edge. Thus the number of ridges corresponds to that of rakers. The ridges of successive arches interdigitate when the branchial apparatus is contracted. Eigenmann (1912: 258) referred to these epithelial structures as "broad laminae with papillated ridges." The ridges are well shown in the photographs of the gill arches accompanying Eigenmann's original description (op. cit., pl. 33, figs. 2–4). In these figures the gill rakers themselves are poorly or not at all discernible except on the lower portion of the first gill arch (fig. 2a).

The functional anatomy of the hyoid and branchial arches should be examined in live *Bivibranchia.* To judge from alizarin preparations, the hyoid arch may move independently of the branchial arches, using basibranchial 1 as a pivot. When the hyoid arch is forward, basibranchial 1 lies horizontally. When the hyoid arch is pushed backward, basibranchial 1 assumes a vertical orientation with its posterior end directed ventrally (Figs. 34, 35). This presumably would effect the pharyngeal pumping mechanism.

Pharyngeal teeth (Figures 31–34, 36–37). In *Argonectes* pharyngeal toothplates and pharyngeal dentition generalized. Upper pharyngeal dentition occurs on four pairs of separate toothplates that are intimately associated with ventral surface of infrapharyngobranchials 2, 3 and 4 and epibranchial 4. Lower pharyngeal dentition restricted to a pair of toothplates of fifth ceratobranchials. Dentition on all toothplates consisting of dense patches of moderate-sized simple conical teeth.

In *Bivibranchia* pharyngeal dentition highly specialized. Upper pharyngeal dentition restricted to a single pair of toothplates loosely associated with medially directed processes of infrapharyngobranchial 3 and epibranchials 3 and 4 (infrapharyngobranchial 4 absent). Upper toothplate of each side bearing two nearly coextensive, close-set rows of eight to ten tricuspid, pedicellate teeth (rows more regular in 115.2-mm specimen than in 39.9-mm specimen). Lower pharyngeal dentition restricted to a single pair of toothplates intimately associated with dorsal surface of ceratobranchial 5. Lower pharyngeal dentition consisting of three or four irregular rows of pedicellate teeth. In 39.9-mm specimen only anteriormost tooth row consisting of tricuspid teeth, remaining teeth unicuspid. In 115.2-mm specimen first two or three tooth rows almost entirely tricuspid, last row unicuspid. Tricuspid pharyngeal teeth morphologically similar to jaw teeth. Teeth on upper pharyngeal toothplates of equal size throughout tooth rows; teeth on lower toothplates substantially larger towards middle of pharynx.

Weberian apparatus. Weberian apparatus similar to that in *Hemiodus,* apparently without modifications useful for phyletic analysis within Hemiodontidae.

Pectoral girdle. Pectoral girdle of

generalized characoid morphology, similar to that of *Hemiodus*, except for postcleithra of *Bivibranchia*. In *Argonectes* three postcleithra, similar in shape and size to those of *Hemiodus*. In *Bivibranchia* only two postcleithra, corresponding to postcleithra 2 and 3 in other characoids. Shape of postcleithrum 3 as in *Hemiodus*, strutlike distally, with a proximal lamina. Shape of postcleithrum 2 specialized, with a strutlike extension dorsally.

Pelvic girdle. Shape of pelvic girdle similar to that in *Hemiodus*. Base of ischiac process directed medially, perpendicular to pelvic bone. *Argonectes* with 12 pelvic rays, *Bivibranchia* with ten.

Vertebral counts. Total vertebral and precaudal plus caudal vertebral counts: *Argonectes*, 43 (24 + 19); *Bivibranchia*, 40(22 + 18) (in two specimens).

Caudal skeleton (*Figures 38–39*). Caudal skeleton of typical hemiodontid morphology.

ANODONTINAE

Cranium (*Figures 40–42*). Cranium relatively narrow and shallow. Frontoparietal fontanel complete; frontal portion about half as wide as parietal portion and uniform in width for most of its length, widening slightly immediately in front of epiphyseal bar. Frontal portion prolonged anteriorly by opening between diverging posterior limbs of ethmoid bone (Fig. 40). Ethmoid moderately wide, more so than in Hemiodontinae but much less than in Curimatidae, its anterior end with processes articulating with premaxillaries and maxillaries (as in *Hemiodus*). Supraoccipital crest flattened dorsally but narrower than in *Hemiodus* and failing to reach end of cranium. Exoccipitals and basioccipital extend considerably further posteriorly than supraoccipital crest. Posttemporal fossae with three openings as in Hemiodontidae, Curimatidae and many other characoids. Dilator groove well developed, opening broadly onto dorsal surface of cranial roof. Posterior margin of epiotic strongly angulated but without posteriorly directed spine. Pterotic with very elongate, slender, posteriorly directed process.

Vomer with a relatively flat ventral surface (no ventrally directed median ridge), and a pair of relatively small, separately formed lamellae on its dorsal surface, these dorsolateral elements considerably smaller than comparable elements present in Hemiodontinae (comparable elements absent in Curimatidae?) Ventral portion of vomer with strongly demarcated anterior and posterior portions; anterior portion circular in ventral view, posterior portion circular anteriorly but drawn out to a point posteriorly. Parasphenoid relatively straight, gently sloping upwards anteriorly, with a poorly developed, ventrally directed median lamella. Posterior portion of parasphenoid cleft for about one-eighth of its length only (cleft for all or almost all of its length in other Hemiodontidae). Lateral ethmoids similar in shape to those in Hemiodontinae, although somewhat smaller, and with anterior processes articulating with vomer more elongate. Rhinosphenoid present. Interorbital septum smaller than in Hemiodontinae. Subtemporal fossa shallow but distinct. Intercalar bone large, with a short, posteriorly directed process bearing ligament of attachment with lower limb of posttemporal bone. Auditory fenestra large. Lagenar capsules moderate in size (not greatly enlarged as in Curimatidae).

Otoliths (*Figure 43*). All three otoliths in Anodontinae relatively elongate compared to those in *Hemiodus* and *Brycon*. Lapillus enlarged, even larger than asteriscus.

Facial bones (*Figures 44–45*). Circumorbital series complete. Infraorbital 4 with a posteriorly directed canal from infraorbital branch of cephalic laterosensory system. Infraorbitals flat and relatively small, especially infraorbital 6, leaving much of cheek (nearly all of preopercle) exposed. Nasal bone an elongate open canal or trough, without a lamellar portion. Antorbital small, contacting supraorbital but separated by a gap from infraorbital 1. Opercle and interopercle relatively large; gill cover prolonged posteriorly by subopercle (similarly developed opercular bones occur in curimatids such as *Gasterotomus* and *Suprasinelichthys*). Dorsal border of opercle notched, as in Hemiodontinae (in Curimatidae dorsal margin of opercle invariably rounded). Lateral surface of opercle without a flange external to hyomandibulo-opercular joint but with an oblique flange just behind and parallel to its anterior margin (Fig. 44).

Jaws (*Figures 44–45*). Jaws toothless in adults and in smallest specimens known thus far (down to 46.4 mm). Gape large, extent of mouth-opening greater than in any other Hemiodontidae or in any Curimatidae. Premaxillary small, maxillary and dentary enlarged. A large oval fenestra near anterior margin of dentary. Articular bone moderately elongate. A small, horizontally oriented slit where dorsal margin of articular passes internally to dentary. Coronomeckelian bone small, its position relatively ventral (not elevated as in Bivibranchiinae and Parodontidae).

Suspensorium (*Figure 45*). Palatine small, immovably attached to ectopterygoid. Ectopterygoid slender, failing to contact quadrate posteriorly. Mesopterygoid greatly expanded, immovably (?) attached to ectopterygoid and metapterygoid but movably attached to quadrate. Symplectic and posterior limb of quadrate elongate. Metapterygoid-quadrate fenestra large. Metapterygoid without anteroventral limb forming posteroventral border of metapterygoid-quadrate fenestra. Main body of hyomandibular vertically oriented, its anteroventral border greatly indented or concave; posterior end of metapterygoid lying in this indentation but failing to contact hyomandibular.

Hyoid and branchial arches (*Figures 48–50*). Basihyal slender and elongate, seemingly a single ossification. Hyoid bar, especially ceratohyal, relatively elongate. Interhyal small. Dorsal and ventral hypohyals separated from each other slightly, not so closely fitted together as in other hemiodontids. Ceratohyal with dorsal and ventral processes extending from its anterior end and applied to lateral surface of dorsal and ventral hypohyals, respectively (Fig. 48). Five branchiostegal rays; four on ceratohyal and one on epihyal. Proximal end of branchiostegal ray 4 not greatly expanded. Branchiostegal rays elongate and moderately slender. Urohyal extremely elongate. Lateral wings of urohyal narrow and strongly depressed (ventral surface of urohyal deeply indented). Dorsomedian lamina of urohyal well developed, its crest extending posteriorly beyond lateral wings (Fig. 48).

Branchial arches with three basibranchials and three hypobranchials, basibranchials 1–3 and hypobranchials 1–3 successively more elongate. Basibranchial 1 very small, basibranchial 2 moderately elongate, and basibranchial 3 extremely elongate (twice as long as basibranchial 2). Hypobranchials 1 and 2 flat or nearly so; hypobranchial relatively elongate, its dorsal surface moderately excavated (much less so than in *Hemiodus*). Ceratobranchials 1–4 successively shorter; ceratobranchial 1 very elongate; ceratobranchial 4 distinctly shorter and ceratobranchial 5 narrower than ceratobranchials 1–3. Four epibranchials and three infrapharyngobranchials (a very thin, slivery and elongate ossification where infrapharyngobranchial 4 would be located is interpreted as an upper pharyngeal toothplate; it bears minute teeth and is similar to lower pharyngeal toothplate in appearance). Epibranchials 1–3 and infrapharyngobranchials 1–3 with well-developed apophyses. Infrapharyngobranchials 1–3 successively larger, infrapharyngobranchial 3 twice as long as infrapharyngobranchial 2. Pharyngeal dentition consisting of minute conical teeth rather widely spaced on elongate and extremely narrow toothplates.

Gill rakers (*Figures 48–51*). Numerous gill rakers on both leading and trailing edges of first four gill arches and on leading edge of fifth gill arch (ceratobranchial 5). Gill rakers of arch 5 interdigitating with those on trailing edge of arch 4 and extending distally into a sort of pocket or epibranchial organ, although arrangement of distal gill rakers basically similar to that in other Hemiodontidae and in Parodontidae (cf. Fig. 13 of *Hemiodus* and Fig. 74 of *Saccodon*). Rakers very elongate and slender, directed foreward at an acute angle; long axis of rakers on leading and trailing edges of first three gill arches closely parallel. One margin of each raker smooth, with a narrow membranous flap for its entire length; opposite margin armed with a double row of minute ctenii. Rakers on leading edges of arches with ctenii directed medially, opposing laterally-directed ctenii on rakers of trailing edges. Ctenii increasing in number with age. In a 55.0-mm *A. melanopogon* most rakers about 3 mm long, with a double row of 40 + 40 ctenii. A 212-mm individual has most rakers about 11 mm long, with just over 130 + 130 ctenii. A 200-mm *A. elongatus* has most rakers about 10 or 11 mm long, with about 130 + 130 or more ctenii. In large specimens ctenii approximately 0.2–0.3 mm long and 0.1 mm or less apart (Fig. 51). Rakers of successive arches not diminished in size, and with ctenii equally numerous. Rakers on trailing edge of arches as long as those on leading edge.

Number of rakers increasing with age, first arch with 90–100 rakers in specimens of 50–55 mm and almost 200 in large specimens. A 55.0-mm *A. melanopogon* has 35 + 1 + 62 rakers on its first arch, a 212-mm specimen 73 + 1 + 115; a 200-mm *A. elongatus* has 80 + 1 + 110. Number of rakers on upper limb of arch greater in arches 2–4 than in arch 1. *A. melanopogon* of 55.0-mm with 35 + 1 + 62 rakers on arch 1 has 48 + 1 + 65 on arch 2, 58 + 1 + 51 on arch 3, and 51 + 1 + 63 on arch 4. Rakers at extremes of arches may extend beyond bones of arches, most notably on lower limb of arch 4, where a long series of rakers extends anteriorly from anteromedial end of ceratobranchial (Fig. 50) (no comparable series of rakers in *Hemiodus*).

Weberian apparatus (*Figure 52*). Weberian apparatus differing from that of *Hemiodus* only in details of shape and proportion of some parts, most notably neural complex, which is very elongate and low-lying.

Pectoral girdle (*Figure 53*). Pectoral girdle complete, each half with extrascapular, posttemporal, supracleithrum, cleithrum, three postcleithra, mesocoracoid, coracoid, scapular, four proximal radials, and an irregular series of small distal radials (not figured). Postcleithra relatively small but shaped as in *Hemiodus*. Coracoid small, failing to contact anterior end of lower limb of cleithrum. Posttemporal, supracleithrum and upper limb of cleithrum unusually slender and elongate, as in curimatids such as *Gasterotomus* and *Suprasinelichthys*, which have greatly expanded gill covers and gill openings superficially similar to those of *Anodus*.

Pelvic girdle (*Figure 54*). Pelvic girdle similar to that in *Hemiodus*. Pelvic bone slightly narrower and ischiac process more elongate than in *Hemiodus*. Pelvic fin with 11 rays.

Vertebral counts. Anodontinae exhibit total vertebral and precaudal plus caudal vertebral counts as follows: *A. elongatus*, 45 (32 + 13); *A. melanopogon*, 44 (29 + 15) and 45 (29 + 16).

Caudal skeleton (*Figure 55*). Caudal skeleton of generalized hemiodontid morphology. Three slender epurals. Hypurals 1 and 2 fused to each other and both separate from ural centrum. Principal caudal rays 10 + 9.

Parodontidae

Cranium (*Figures 56–59*). Cranial roof including supraorbital portion of frontal bone convex and smooth. Frontal and parietal bones of opposite sides broadly overlapping at midline of cranium for their entire length (frontoparietal fontanel absent). Dilator fossa roofed by frontal bone, not extending onto dorsal surface of cranium. Ventroposterior extension of supraorbital process of frontal bone with a large foramen open into dilator fossa. Ventral rim of foramen formed by a thin semicircle of bone. Supraoccipital crest absent; posterior margin of supraoccipital either with a bifid dorsal process (*P. guyanensis, A. affinis*), bilateral, horizontal flanges (*P. caliensis*), or evenly rounded (*Saccodon*). Posttemporal fossa with three openings (as in Hemiodontidae, Curimatidae, etc.). Head of ethmoid with a thin ventromedian lamella and lateral projections for articulation of movable premaxillaries. Posterior portion of ethmoid with a strong ventromedian process broadly joined to vomer. Ethmoid and vomer rigidly joined to each other; posterior laminae of ethmoid loosely attached to ventroanterior surface of frontals, apparently moving freely beneath them. Articulation of vomer with parasphenoid and lateral ethmoids apparently movable (permitting head of ethmoid to move in a vertical plane?). Rhinosphenoid absent. Orbitosphenoid enlarged, ventroanterior process of orbitosphenoid sutured to posteromedially directed processes from lateral ethmoids, orbitosphenoid failing to contact parasphenoid. Anterior portion of parasphenoid straight, not curving upwards as in Hemiodontidae and many other characoids. Hyomandibular fossa developed on lateral margin of prootic bone and anterior portion of pterotic (in most characins, including Hemiodontidae, the main articular surfaces of the hyomandibular fossa are on the sphenotic and pterotic). Subtemporal fossa well developed, lying entirely on pterotic bone. In *Saccodon* exoccipitals with a narrow but deep bony ridge extending laterally from lagenar capsules to intercalar bone. Lagenar capsules reduced in size. Intercalars relatively large. Epiotic with moderately elongate posterior process. Posterior process of pterotic short and rounded.

Otoliths (*Figure 60*). Otoliths of relatively generalized characoid morphology, not greatly different in size and shape from those in *Brycon*.

Facial bones (*Figures 61–65, 70*). Nasal bone slender and moderately elongate, almost entirely tubular. Circumorbital series complete, with a supraorbital, antorbital and six relatively large infraorbitals. Antorbital a small, triangular element, its apex separated by a slight gap from supraorbital, its base resting on dorsal margin of infraorbital 1. Infraorbital 1 covering posterior portion of premaxillary. Infraorbital 2 covering most of dentary. Infraorbitals 2–4 almost entirely hiding preopercle from view. Ventral portion of infraorbitals 2 and 3 curving strongly underneath head.

Opercular series complete, with a preopercle, interopercle, subopercle and opercle. No supraopercle or suprapreopercle. Lateral surface of opercle smooth, dorsal margin of opercle broadly rounded. Posterior portion of interopercle greatly deepened. Subopercle relatively shallow for its entire length, with a well-developed ascending process internal to "junction" of preopercle, opercle and interopercle. Anterior end of preopercle immovably joined to quadrate; anterolateral surface of preopercle completely covered by bony extension of quadrate. Opercle and subopercle oriented parallel to main axis of head. Anterior ends of preopercle and interopercle inclined inwards towards quadrato-mandibular junction.

Jaws and jaw teeth (*Figures 63–71*). Premaxillaries greatly expanded, with from $2 + 2$ to $5 + 5$ functional teeth in a single row. Replacement tooth trenches for each functional tooth position separated from each other by bony ridges on inner face of premaxillaries with from four to 30 preformed replacement teeth. Replacement teeth largely enclosed by lateral and median walls of premaxillary and in varying degrees by a ventrally directed extension arising from dorsoposterior margin of premaxillary. In *Apareiodon affinis* this extension is short and replacement teeth lie relatively exposed posteriorly. It extends further ventrally in *Parodon caliensis.* In dental morph I of S. *wagneri,* entire dorsoposterior margin of premaxillary extends ventrally to cover almost half of extent of replacement tooth rows. In dental morph IV of S. *wagneri* dorsoposterior margin of premaxillary extends ventrally to cover two-thirds of extent of replacement tooth rows. Flattened median walls of premaxillaries of opposite sides firmly united to each other by tough connective tissue. Premaxillaries with dorsomedian process articulating to ethmoid. Dorsomedian processes greatly expanded in *A. affinis* and *P. caliensis,* moderately expanded in *P. guyanensis,* and relatively small in S. *wagneri.* A longitudinal depression or groove in dorsal surface of premaxillary, lateral to dorsomedian process, into which fit lateral projections from head of ethmoid.

Maxillary relatively small and slender, strongly curved, edentulous or with one to three small teeth. One preformed replacement tooth for each functional tooth lies in a pocket in maxillary. Ascending process of maxillary loosely attached to premaxillary. Some specimens of S. *wagneri* with a small supramaxillary at tip of ascending premaxillary process.

Lower jaw extremely similar in form to that in Hemiodontidae, albeit of relatively stouter construction. Dentaries with an oval fontanel near anterior margin, slender symphysial processes joined to each other by tough connective tissue, and elevated lateral walls just inside rictus of jaws. Dentary either toothless (*Apareiodon, Saccodon,* young *Parodon*) or with one to three large stout teeth planted on inner surface of lateral expansion just inside rictus of jaws. Articular bone and posterior portion of dentary slender. Coronomeckelian bone large, its position near dorsal edge of articular much higher than in most other characoids.

Suspensorium (*Figures 63–65, 70, 72*). Palatine large, its anterior end expanded, its posterior end immovably attached to ectopterygoid and lying in a long trough or groove in dorsoanterior surface of ectopterygoid. Ectopterygoid moderately expanded anteriorly, slender posteriorly, its posterior end forming a narrow, movable joint with dorsal edge of quadrate. Mesopterygoid movably articulated with median surfaces of ectopterygoid and metapterygoid. Posterior portion of metapterygoid loosely bound to hyomandibular. Metapterygoid-quadrate foramen moderately large. Anterior end of hyomandibular inclined inwards towards quadrato-mandibular joint. Quadrate firmly united to preopercle, a bony extension from quadrate overlying lateral surface of anterior end of preopercle. Quadrato-mandibular condyle very large. Lateral surface of quadrate posterior to condyle greatly thickened.

Hyoid and branchial arches (*Figures 73, 74*). Basihyal moderately elongate, narrow posteriorly and slightly expanded anteriorly. Hyoid bar of generalized characoid morphology. Dorsal and ventral hypohyals separate (not fused together). Interhyal relatively small. *Apareiodon* with three branchiostegal rays, *Saccodon* and *Parodon* with four. In *Saccodon* branchiostegal rays 1 and 2 ending basally in slender flanges articulating on inner surface of ceratohyal. Branchiostegal rays 3 and 4 with relatively stout basal flanges articulating with external surface of ceratohyal and epihyal, respectively. Urohyal short and stout, its horizontal laminar portions relatively broad, its dorsal median lamina terminating in a high crest.

Three basibranchials. Basibranchial 1 short, basibranchials 2 and 3 elongate. Three hypobranchials. Hypobranchial 1 flat, hypobranchials 2 and 3 with strongly concave dorsal surfaces. Epibranchials and ceratobranchials relatively shorter than in Hemiodontidae. Epibranchials oriented almost at a right angle to main axis of body when viewed from above; ceratobranchials at an angle of about 45 degrees. Three infrapharyngobranchials;

infrapharyngobranchials 2 and 3 moderately enlarged.

Gill rakers moderately elongate or short and platelike, without ctenii. Number of gill rakers moderate, increasing slightly with age. *Saccodon wagneri* of 50 to 55 mm have 32–35 gill rakers on first gill arch. A 103.3-mm specimen of dental morph IV with gill rakers on leading and trailing edges of gill arches as follows: arch 1, 20 + 1 + 22 on leading edge and 30 + 27 on trailing edge; arch 2, 15 + 1 + 39 and 23 + 1 + 36; arch 3, 32 + 1 + 42 and 23 + 43; arch 4, 23 + 46 + (?) and 0 + 35; and arch 5, 0 + 28 (on leading edge only of ceratobranchial 5). A 63.5-mm *Parodon caliensis* has 16 + 1 + 23 rakers on leading edge of arch 1, a 46.8-mm *Apareiodon affinis*, 12 + 1 + 22. In *A. affinis* gill rakers on leading edge of arches 2 and 3 enlarged, much larger than those on arch 1; in other parodontids examined, largest rakers occur on leading edge of arch 1 (Fig. 74). Row of gill rakers on leading edge of ceratobranchial 5 terminating distally in a semicircle of rakers of diminutive size, joining a complementary semicircle of similar rakers from trailing edge of ceratobranchial 4 (Fig. 74). A comparable condition occurs in Hemiodontidae (Hemiodontinae and Anodontinae) and perhaps in other characoids.

Pharyngeal dentition consisting of numerous, small conical teeth, apparently non-pedicellate, well developed only on last pair of upper pharyngeal toothplates (those loosely associated with medial ends of epibranchials 3 and 4) and on lower pharyngeal toothplates associated with dorsal surface of ceratobranchial 5. Toothplates on ventral surface of infrapharyngobranchials 2 and 3 either absent or small and with few teeth.

Weberian apparatus (*Figure* 75). Weberian apparatus similar to that in numerous characoids, apparently without useful features for phyletic studies.

Pectoral girdle (*Figure* 76). In *A. affinis* pectoral girdle, including postcleithra 1–3, relatively similar to morphologically generalized pectoral girdle of *Hemiodus* (no close relationships implied). In *Saccodon* and *Parodon* cleithrum enlarged, its anterior and posterior limbs curving strongly inwards; medially directed lamina from anterior and ascending limbs of cleithrum very strong; postcleithrum 2 greatly expanded, postcleithrum 3 strutlike, narrow for its entire length. In *Saccodon,* first two pectoral fin rays simple; in *Parodon* and *Apareiodon* only first pectoral ray simple.

Pelvic girdle (*Figure* 77). Anterior portion of pelvic bone simple (not bifid or trifid), broader in *Saccodon* than in *Apareiodon* or *Parodon.* Ischiac process relatively short and simple in *Saccodon.* In *P. caliensis* and *A. affinis* ischiac process elongate and thin posteriorly, especially in *P. caliensis,* and bearing a short, lateral projection near its base. Eight or nine pelvic fin rays.

Vertebral counts. Parodontidae exhibit total vertebral counts and precaudal plus caudal vertebral counts as follows: *P. caliensis* 35 (14 + 21); *A. affinis* 41 (20 + 21, 21 + 20); dental morph I of *S. wagneri* 38 or 39 (18 + 20, 20 + 18, 19 + 20); and dental morph IV of *S. wagneri* 38 (18 + 20 in two specimens, 19 + 19, 20 + 18).

Caudal skeleton (*Figure* 78). Caudal skeleton morphologically generalized for characoids, similar to caudal skeleton of most Characidae, Curimatidae, etc. Epurals two. Uroneurals two. Hypurals six; hypural 2 slender, separate from hypural 1, fused to complex ural centrum (as in most characoids). Principal caudal rays 10 + 9.

DISCUSSION

Relationship Between Hemiodontidae and Parodontidae

The superficially similar appearance of Hemiodontidae and Parodontidae together with the unique disposition of the jaw teeth common to many species in both families, has led most students of characoid classification to regard them as closely related

TABLE 2. DISTINGUISHING CHARACTERISTICS OF PARODONTIDAE AND HEMIODONTIDAE

	Parodontidae	Hemiodontidae
Premaxillary	Highly mobile.	Immobile or only slightly mobile.
	Greatly enlarged.	Minute to considerably enlarged but never as much as in Parodontidae.
	From four to over 30 preformed replacement teeth for each functional tooth lying in trenches with bony partitions.	A maximum of four to six preformed replacement teeth for each functional tooth; no trenches or bony partitions separating them.
Maxillary	Lies entirely lateral to premaxillary, without contacting ethmoid.	Tends to articulate directly with ethmoid.
Frontoparietal fontanel	Absent.	Present.
Rhinosphenoid	Absent.	Present.
Adipose eyelid	Absent.	Present.
Branchiostegal rays	Three or four.	Four or five.
Hypural 2	Fused to ural centrum and separate from hypural 1.	Separate from ural centrum and fused to hypural 1.
Vertebrae	35 to 41.	40 to 45.

(Regan, 1911; Eigenmann, 1912; Fowler, 1950; Géry, 1959; Greenwood et al., 1966). Only Regan (1911) and Géry (1959) presented osteological evidence bearing on this problem, and their evidence is brief and not very informative. Regan pointed out some similarities in the suspensorium (similarities shared with the unrelated forms *Nannostomus* and *Characidium*), stated that the hyomandibular is single-headed (I find it bicipital in both families), and incorrectly indicated that the maxillaries in both Hemiodontidae and Parodontidae articulate with the ethmoid (in some Hemiodontidae the maxillaries articulate with the ethmoid, but in Parodontidae they lie entirely lateral to the expanded premaxillaries). Géry (1959) compared the superficial cranial features of *Parodon guyanensis* with those of *Hemiodus quadrimaculatus* and found them similar in a number of respects but the similarities involved do not include any specialized features.

The similarity of the jaws (especially the lower jaws) and dentition of many Parodontidae and Hemiodontidae is undeniably striking. The shape of the upper jawbones in *H. quadrimaculatus,* together with the decrease in number of functional teeth and increase in replacement teeth in this species (Fig. 10), does suggest a step towards the highly specialized premaxillaries and maxillaries of Parodontidae. On the other hand, the premaxillaries of *H. quadrimaculatus* show no indication of bony septae separating the replacement teeth for each functional tooth position (such septae are diagnostic of Parodontidae). The similarity in shape of the lower jaws in the two families can be seen by comparing Figures 7 and 8 with 65 and 70. The specialized suspensorium is also very similar. The slightly overlapping condition of the quadrate with the anterior end of the preopercle in Hemiodontinae suggests a step towards the highly specialized condition in Parodontidae (compare Figs. 11 and 72). It seems, however, that phyletically suggestive osteological similarities do not extend beyond the jaws and suspensoria. The cranium of Parodontidae is highly specialized and differs in many respects. The hyoid and branchial arches, Weberian apparatus, pectoral and pelvic girdles and vertebral columns in both families are of relatively generalized characoid morphology and do not seem to offer useful characters in the present context. The caudal skeleton of Parodontidae is more generalized than that of Hemiodontidae in having hypurals 1 and 2 separate and hypural 2 fused to the ural centrum. Whether Hemiodontidae and Parodontidae are indeed close relatives will have to be resolved by further study. In any event, there are considerable differences between the two families (Table 2).

Transfer of Anodontinae from Curimatidae to Hemiodontidae

Anodontinae has been placed in Curimatidae by most students of characoid classification (Eigenmann and Eigenmann, 1889; Regan, 1911; Fernandez-Yepez, 1948; Greenwood et al., 1966) because its members lack jaw teeth and superficially resemble curimatids such as *Gasterotomus*. Evidence that Anodontinae should be transferred from Curimatidae to Hemiodontidae can be marshalled as follows:

1. Curimatidae are characterized by a strong flange on the lateral surface of the opercle, just above the hyomandibulo-opercular joint (Fig. 46). This feature is readily observable, without dissection, in alcoholic specimens, and is present in all species of Curimatidae seen by me. I do not know of any other characoids with a comparable opercular flange. The flange is absent in *Anodus*.

2. In the lower jaw of Curimatidae the articular is relatively short; both the dentary and articular are elevated; where the dentary and articular join there is a large vertical gap or fenestra, and there is no oval fenestra in the dentary (Figs. 46–47). In Hemiodontidae the articular is relatively elongate; the dentary is elevated in varying degrees, but the articular is never elevated; where the dentary and articular join there are either no gaps or only horizontally oriented gaps (cf. *Bivibranchia*), and there is an oval fenestra in the dentary. In all of these features the lower jaw of *Anodus* agrees with that of Hemiodontidae. *Anodus* has an exceptionally large oval fenestra in the dentary.

3. In Curimatidae the gill rakers are absent or poorly developed: with little or no ossification, short and "fleshy" and relatively few in number. In most hemiodontids the gill rakers are well developed: well ossified, elongate, often bearing ctenii, and relatively numerous. The gill rakers of *Anodus* are exceptionally well developed: well ossified, very elongate, provided with minute ctenii, and more numerous than in any other characoids (increasing in number with age).

4. Curimatidae usually (always?) have four branchiostegal rays. Hemiodontidae often have five branchiostegal rays (four or five in *Hemiodus*, five in *Micromischodus*, *Argonectes*, *Bivibranchia*). *Anodus* has five branchiostegal rays. In Curimatidae the branchial membranes are united to the isthmus. In Anodontinae and in other Hemiodontidae excepting *Bivibranchia* the branchial membranes are free from the isthmus and the gill openings extend relatively far forward ventrally.

5. Curimatidae are characterized by a joint between the palatine and lateral ethmoid which is absent in Hemiodontidae and Anodontinae. In Curimatidae the dorsal surface of the posterior end of the palatine is expanded into a facet (Fig. 47) which either attaches directly to a facet on the ventral surface of the lateral ethmoid just internal to its lateral wing or else is joined to such a facet by dense connective tissue (sometimes cartilaginous). There is no indication of these facets on the palatine and lateral ethmoid in Hemiodontidae or Anodontinae.

6. Curimatidae are characterized by a greatly enlarged lagenar capsule. In Ano-

dontinae, as in Hemiodontidae, the lagenar capsule is relatively small.

7. In Curimatidae body shape is extremely variable, but rarely, if ever, is it truly subcylindrical and fusiform as in all Hemiodontidae and in Anodontinae. Many curimatids are deep bodied or laterally compressed. The ventral abdominal surface is frequently squared off, keeled, or carinate. The body contour is frequently modified in front of or along the base of the dorsal and anal fins.

8. Of more than 100 species, only one curimatid—*Curimatorbis ocellatus* Eigenmann and Eigenmann 1889—has an oval spot on the middle of the body just behind the dorsal fin. Such a spot is more characteristic of Hemiodontidae, being present in several species of *Hemiodus,* in *Argonectes,* and in two undescribed species of *Bivibranchia* from Surinam (Géry, personal communication). A comparable spot is always present in *A. elongatus* and sometimes present (although faint) in *A. melanopogon* (Plate I).

9. Excepting very small species and young stages, Curimatidae have an intestine with numerous coils. In Hemiodontidae and in *Anodus* the intestine is moderately coiled.

10. Curimatidae have low vertebral counts, from 30 to 36, about evenly divided between precaudal and caudal vertebrae. Anodontinae have 44 or 45 vertebrae, precaudal vertebrae twice as numerous as caudal. Hemiodontidae other than Anodontinae have 40 to 43 vertebrae, and precaudals about twice as many as caudals.

11. In Curimatidae hypural 2 is fused to the complex ural centrum and entirely separate from hypural 1. In *Anodus,* as in Hemiodontidae, hypural 2 is fused to hypural 1 and has lost its connection with the ural centrum.

In comparing the skull of *Anodus* with those of other characoids, one is struck by how much space is occupied by the gill arches and expanded gill covers and how little by the elongate, narrow and relatively depressed cranium. In curimatids such as *Gasterotomus* and *Suprasinelichthys* in which the gill covers are also enlarged and the external appearance of the head strongly resembles that of *Anodus,* the cranium is relatively heavy, broad and deep. The general appearance of the cranium of *Anodus* is more like that of *Hemiodus* than of any curimatids I have examined.

Anodus agrees with both Hemiodontidae and Curimatidae in having three openings into each posttemporal fossa and a rhinosphenoid bone. These characters are of minor phyletic significance, since three openings into the posttemporal fossa occur in many noncharacid characoids, African as well as South American, and the rhinosphenoid is present in many South American groups. The only character shared exclusively by Curimatidae and Anodontinae is absence of jaw teeth, a loss character, and therefore of dubious significance.

The characteristics of Anodontinae are approached in some ways by *Hemiodus microlepis.* The superficial resemblance between this species and *A. elongatus* is as striking as that between *A. elongatus* and curimatids such as *Curimatorbis ocellatus* or *Gasterotomus latior. H. microlepis* has about 105–115 scales in a lateral series and an oval spot on the body just posterior to the dorsal fin. The gill rakers, although not elongate as in *A. elongatus,* are relatively numerous (probably increasing in number with growth) and denticulate. A 235-mm specimen has 30 + 40 gill rakers on the first gill arch. Each comblike raker bears about 10 large ctenii (Fig. 14). Fowler (1906: 319) reported 22? + 38? ciliate rakers in a specimen nine inches long. Gill rakers of the last arch are relatively large and interdigitate with trailing gill rakers of the fourth arch, as in other species of *Hemiodus* and in *Anodus.* The teeth, although typical in shape for *Hemiodus,* are relatively small and numerous (about 20–22 on each side

TABLE 3. DISTINGUISHING CHARACTERISTICS OF THE SUBFAMILIES OF HEMIODONTIDAE

	Hemiodontinae	Bivibranchiinae	Anodontinae	Micromischodontinae
Jaw teeth	Upper jaw only. A single row of 16–44 on premaxillary and maxillary. Fan-shaped, pedicellate, ca. 10–20 cusps. Several sets preformed replacement teeth.	Upper jaw only. A single row of 16 on premaxillary and maxillary. Tricuspid, short pedicel. One to four sets preformed replacement teeth.	Absent.	Both jaws. Premaxillary with single row of 28; maxillary toothless; dentaries with two nearly coextensive rows of 100–120. Unicuspid, with minute, recurved cusps, elongate, swollen pedicels. Single set preformed replacement teeth.
Jaws	Nonprotrusible. Premaxillary large, immobile or only slightly movable.	Highly protrusible. Premaxillary minute, firmly attached to anterior end of maxillary, entirely freed from cranium	Nonprotrusible. Premaxillary moderate-sized, immobile or only slightly movable.	Nonprotrusible. Premaxillary moderate-sized, immobile or only slightly movable.
Suspensorium	Generalized. Anterior end immovable, joined to cranium, or capable only of slight movement. Ectopterygoid-quadrate joint generalized.	Highly specialized. Anterior end freely movable downwards and away from cranium. Ectopterygoid-quadrate joint extremely mobile and specialized.	Generalized. Conditions comparable to those in Hemiodontinae.	Generalized. Conditions comparable to those in Hemiodontinae.
Gill rakers	Variable in form and number, usually moderately numerous. Often bearing large, moderately numerous ctenii.	Reduced in size, relatively few in number. Ctenii absent.	Extremely elongate and numerous. Ctenii minute, extremely numerous, disposed in a double row.	Moderately elongate and numerous. Ctenii absent.
Branchiostegal rays	Four or five.	Four.	Five.	Five.

of the upper jaw). The tapered posterior chamber of the swimbladder extends to or slightly beyond the base of last anal fin ray. I have examined two specimens (MCZ 20652; 229 and 235 mm; Tefé, Amazonas, Brazil. Thayer Expedition). The osteology of this species has not been investigated.

The distinguishing characteristics of the Anodontinae and of the other three subfamilies of Hemiodontidae are presented in Table 3.

Remarks on Lower Taxa

Genera of Hemiodontinae. Three genera of Hemiodontinae are currently recognized: *Hemiodus* Müller 1842, *Hemiodopsis* Fowler 1906, and *Pterohemiodus* Fowler 1940. *Anisitsia* Eigenmann and Kennedy 1903 is a synonym of *Hemiodus; Hemiodus* includes only those species in which the scales below the lateral line are larger than those above it (Géry, 1961; 1963b; 1964). The three genera are split very finely. There is a complete gradation between species in which scales above and below the lateral line are the same size and species in which scales below the lateral line are larger. Larger scales below the lateral line occur also in *Micromischodus* (Roberts, 1971: 7, fig. 1) and in many species of Curimatidae. The scales below the lateral line are slightly larger than those above it, even in some species of *Hemiodus* in which they are stated to be of equal size, e.g., *H. microlepis.* In itself this character is insufficient grounds for recognition of a separate genus, and no other distinction between *Hemiodus* and *Hemiodopsis* (cf. Géry, 1964) has been offered. Employment of single characters leads to proliferation of taxa, many of which will be polyphyletic. If a genus is based on such a simple character as scale size there is no way of determining whether it is monophyletic or polyphyletic. For these reasons I do not recognize *Hemiodopsis.* Similar grounds can be given for rejecting *Pterohemiodus,* erected for a species with a filamentous extension of the dorsal fin. Géry (1961: 338) gave a more detailed diagnosis of *Pterohemiodus,* and there is perhaps more reason for retaining this genus than for *Hemiodopsis.* The vertical disposition of the teeth, indicated by Géry as diagnostic of *Pterohemiodus,* is a characteristic feature of *Hemiodus quadrimaculatus* as well as most Parodontidae. Systematic revision of the species of *Hemiodus* is sorely needed. Systematists should note that in this genus the numbers of jaw teeth, of cusps on the jaw teeth, and of gill rakers tend to increase with age.

Genera of Bivibranchiinae. Three genera are currently recognized in Bivibranchiinae: *Bivibranchia* Eigenmann 1912, *Atomaster* Eigenmann and Myers 1927, and *Argonectes* Böhlke and Myers 1956. I have not examined *Atomaster.* Eigenmann and Myers distinguished it from *Bivibranchia* because of its small ctenoid scales. Myers (personal communication) is inclined to think that *Atomaster* is too much like *Bivibranchia* to be recognized as a separate genus.

Böhlke and Myers (1956) regarded *Argonectes* as a closely allied, specialized derivative of *Hemiodus,* having some of the same specializations in the jaws and dentition as *Bivibranchia.* I find that the two genera share several unique specializations in the jaws, jaw teeth and suspensoria, and thus they constitute a well-defined subfamily (see definition above). Their protractile jaws and suspensoria are highly specialized in much the same way, and yet in many respects, even in the structure of the jaws, *Argonectes* is clearly more primitive than *Bivibranchia.* The posterior portion of the maxillary is much more elongate and curved in *Bivibranchia,* perhaps an indication of greater protractility. *Argonectes* lacks the specialized valves found in the roof of the mouth in *Bivibranchia* (and in *Atomaster*) (Eigenmann, 1912; Géry, 1963a; Eigenmann and Myers, 1927). The shapes of the palatine and mesopterygoid, highly specialized in *Bivibranchia,* are relatively generalized or only slightly modified in *Argonectes*. The ectopterygoid-quadrate joint, highly specialized in *Argonectes,* is even more specialized in *Bivibranchia* (compare Figs. 27 and 28). The gill arches, pharyngeal epithelium and pharyngeal dentition, strikingly specialized in *Bivibranchia,* are generalized in *Argonectes,* although *Argonectes* has even fewer gill rakers than *Bivibranchia.* The infraorbital bones and postcleithra, generalized in *Argonectes,* are moderately specialized in *Bivibranchia. Argonectes* has a complete adipose eyelid, *Bivibranchia* the more usual condition in which there is an opening in the adipose eyelid over the pupil. *Argonectes* apparently grows larger than *Bivibranchia.* I have not seen any specimens of *Bivibranchia* larger than 115 mm (the largest reported by Eigenmann, 1912), whereas *Argonectes* attains 198 mm (MCZ 20635), and I have seen specimens from several localities larger than 115 mm.

Genera and species of Anodontinae (Plate I: Frontispiece). Two genera of Anodontinae are currently recognized: *Anodus* Spix 1829 and *Eigenmannina* Fowler 1906. (*Elopomorphus* Gill 1878 is a synonym of *Anodus;* Eigenmann and Eigenmann, 1889.) The generic type of *Anodus* is *A. elongatus* Spix 1829, by monotypy, a well known and widely distributed Amazonian species. *Elopomorphus jordanii* Gill 1878 and *Anodus steatops* Cope 1878 have been placed (correctly, I think) in the synonymy of *A. elongatus* (Eigenmann and Eigenmann, 1889; Fowler, 1906; Fernandez-Yepez, 1948; Fowler, 1950). *"Elopomorphus" orinocensis* Steindachner 1888 (pp. 66–67, pl. 2), from the Orinoco (no other locality given) is probably another synonym of *A. elongatus.* This is the only non-Amazonian record of Anodontinae, and has been overlooked by subsequent authors (Fernandez-Yepez, 1948; Mago Leccia, 1970). (*"Anodus" latior,* recorded from Venezuela by Mago Leccia [1970], is the generic type of *Gasterotomus* Eigenmann 1910 and should be known as *G. latior.* It is a curimatid.)

Only one other species of *Anodus* has been described, *A. melanopogon* Cope 1878, and it is clearly distinct. Widely distributed in the Amazon, it has been taken together with *A. elongatus* in the Río Marañon at Iquitos and in the rio Negro near lago Alexo. It differs from *A. elongatus* in having a more slender build and smaller scales (ca. 125–130 scales in a lateral series vs. 100–105) (Plate I). Specimens of the two species of comparable length seem to have about the same number of gill rakers, but this should be studied in more extensive series than are presently available. *Eigenmannina* Fowler 1906 takes *A. melanopogon* as its generic type, but *A. melanopogon* is so similar to *A. elongatus* that generic separation is unwarranted. I have compared Cope's type specimens of *A. melanopogon* with a series of freshly preserved young specimens of the same size (MZUSP 5959). Although the types are in very poor condition, my examination indicated that they are the same species as the fresh material. The "strongly concave upper profile of the head," used as a generically diagnostic character by Fowler (1906: 306–307, fig. 10), is clearly an artifact of preservation. Both lots have the extensive black coloration on the underside of the jaws, high scale counts and narrow caudal peduncle, and protruding lower jaw that are characteristic of the species. In half-grown and adult specimens of *A. melanopogon* the lower jaw projects only slightly or not at all, as in larger specimens of *A. elongatus.* The largest specimens of *A. melanopogon* examined, 209 and 212 mm, are very similar to *A. elongatus* of the same size.

Genera of Parodontidae. Three genera of Parodontidae are currently recognized: *Parodon* Valenciennes 1849 (*in* Cuvier and Valenciennes, 1849), *Saccodon* Kner and Steindachner 1863, and *Apareiodon* Eigenmann 1916. *Parodontops* Schultz and Miles 1943 has been placed in the synonymy of *Saccodon* as a result of my studies on trophic polymorphism in that genus (Roberts, 1974). *Parodon, Saccodon* and *Apareiodon* are so poorly defined in the literature (cf. Schultz and Miles, 1943; Géry, 1959) that their distinctness may be questioned. *Parodon* differs from the other two genera in having teeth in the lower jaw; according to Géry (1959), the cusps on the premaxillary teeth are more deeply incised. Schultz and Miles stated that the lower jaw is sometimes toothless in young specimens of *Parodon* and questioned the validity of *Apareiodon*. *Saccodon* differs from the other two genera in having two unbranched rays in each pectoral fin instead of only one (Roberts, 1974). Since my observations have been extended to only two species of *Parodon* and two of *Apareiodon* (see Material Examined), I lack sufficient information to provide meaningful definitions of Parodontidae at the generic level.

CONCLUSION

Modification of trophic structures obviously has played a major role in the adaptive radiation of Hemiodontidae and Parodontidae. The four subfamilies of Hemiodontidae are definable primarily in terms of trophic adaptations. Diversification of jaw teeth, complete loss of jaw teeth, radical innovations in functional anatomy of the jaws, and modification of oral and pharyngeal epithelia, of gill rakers, of pharyngeal teeth, and even of endoskeletal elements in the gill arches have occurred. Within Hemiodontidae, Hemiodontinae and Micromischodontinae, although specialized in certain respects, are relatively generalized. In Bivibranchiinae *Argonectes* is clearly more primitive than *Bivibranchia* in many important respects. I see no reason to doubt that *Bivibranchia* had ancestors extremely similar to the living *Argonectes*. Bivibranchiinae differ radically from all other characoids in their highly modified suspensoria and protrusible upper jaws. If *Argonectes* or a form very similar to it gave rise to *Bivibranchia*, then the development of protrusibility set the stage for further modification of the suspensorium and for structural innovations in the oral and pharyngeal epithelia, endoskeletal gill arch elements and pharyngeal dentition found in *Bivibranchia*. In no other characoids are the trophic structures more highly modified than in *Bivibranchia*. Hemiodontinae are generalized enough relative to Bivibranchiinae to have been near the ancestral line to *Argonectes*. Apart from lacking jaw teeth, Anodontinae have little in common with Curimatidae. Unlike Curimatidae (which feed on the bottom and ingest quantities of mud) and other Hemiodontidae (which also feed mainly on the bottom but more selectively than Curimatidae), Anodontinae presumably strain small organisms from midwater. Examination of the guts of preserved *Anodus* reveals only that they do not ingest any mud. Determination of their food items will probably require microscopic examination of fresh stomach contents. Hemiodontidae and Parodontidae offer excellent opportunities for multidisciplinary investigations of the role of feeding habits and trophic adaptations in the evolution of higher taxonomic categories.

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FIGURES

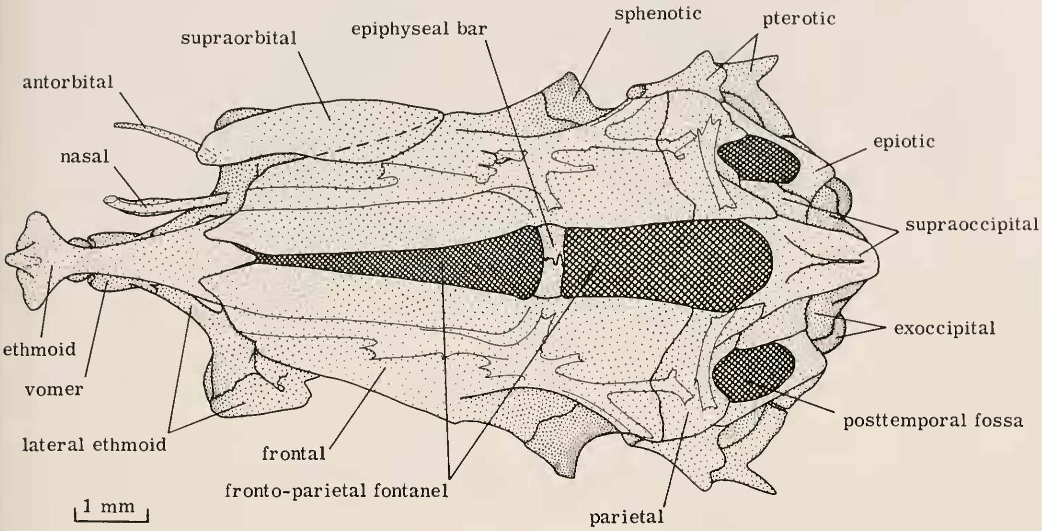

Figure 1. *Hemiodus semitaeniatus*, 55.8 mm. Cranium with nasal bone, antorbital and supraorbital of the right side in place (dorsal view).

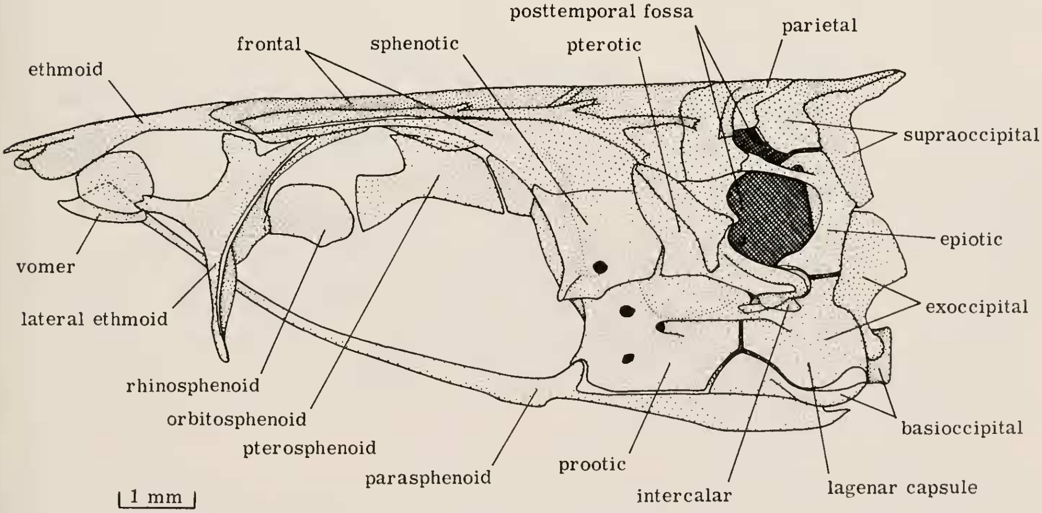

Figure 2. *Hemiodus semitaeniatus*, 55.8 mm. Cranium (lateral view).

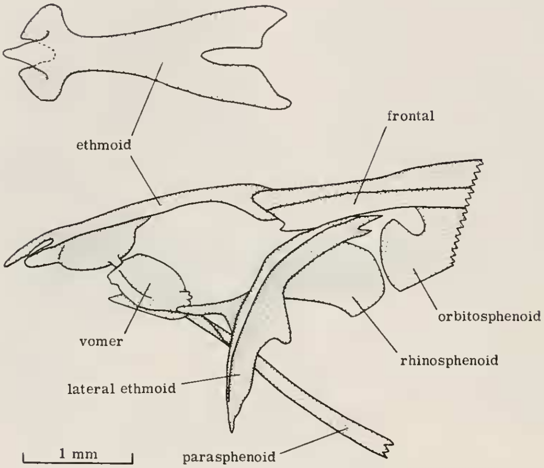

Figure 3. *Hemiodus quadrimaculatus*, 35.0 mm. Anterior portion of cranium (lateral view); inset, ethmoid bone (dorsal view).

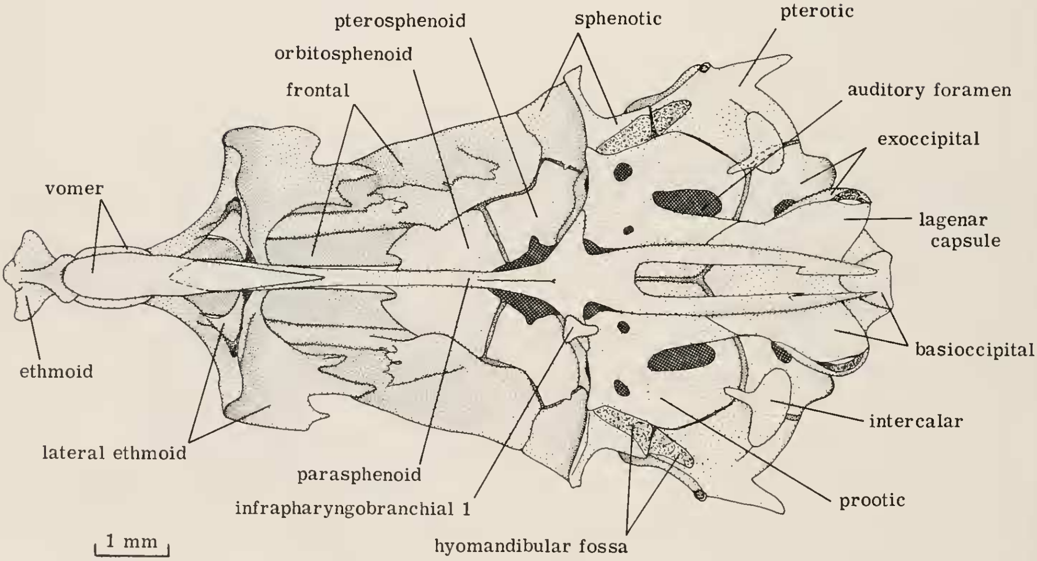

Figure 4. *Hemiodus semitaeniatus*, 55.8 mm. Cranium with infrapharyngobranchial 1 of the right side in place (ventral view).

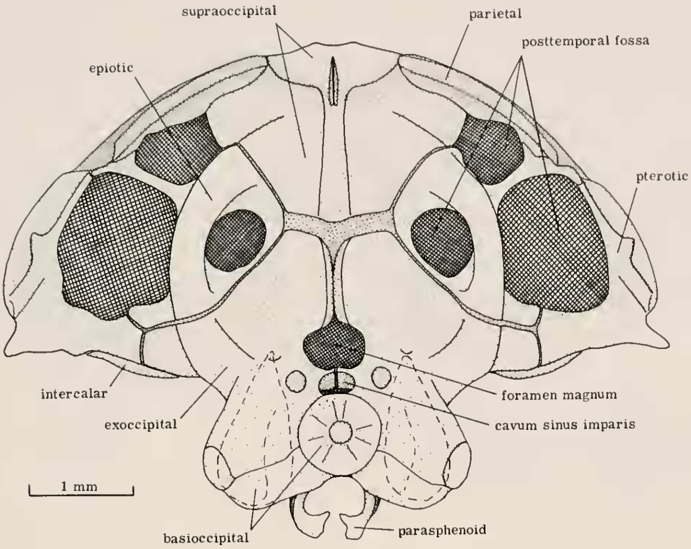

Figure 5. *Hemiodus semitaeniatus*, 55.8 mm. Cranium (occipital view).

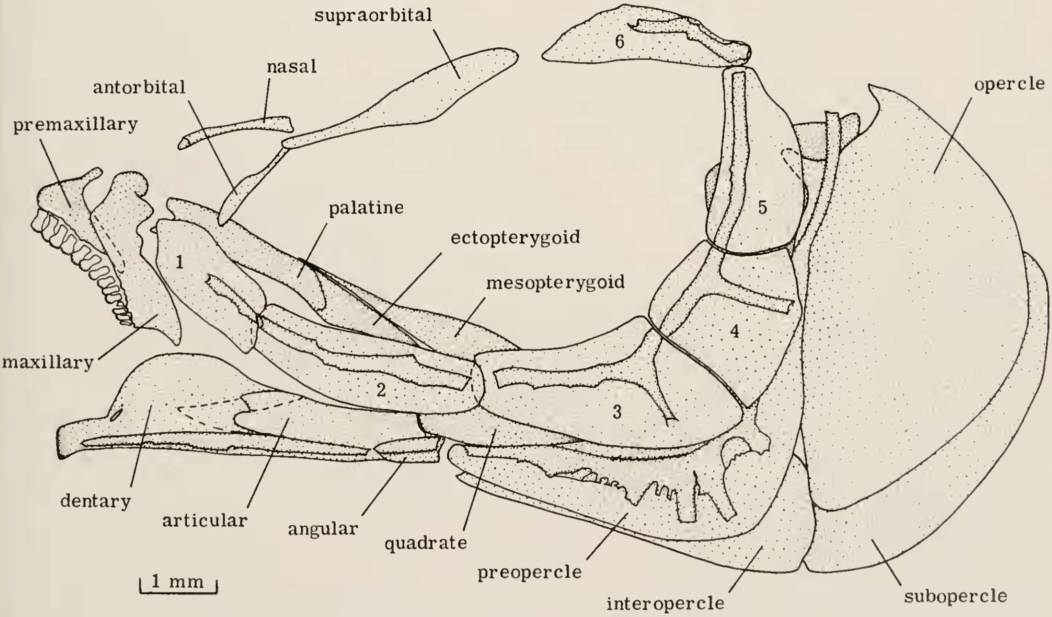

Figure 6. *Hemiodus semitaeniatus*, 55.8 mm. Jaws, facial bones, and suspensorium (lateral view).

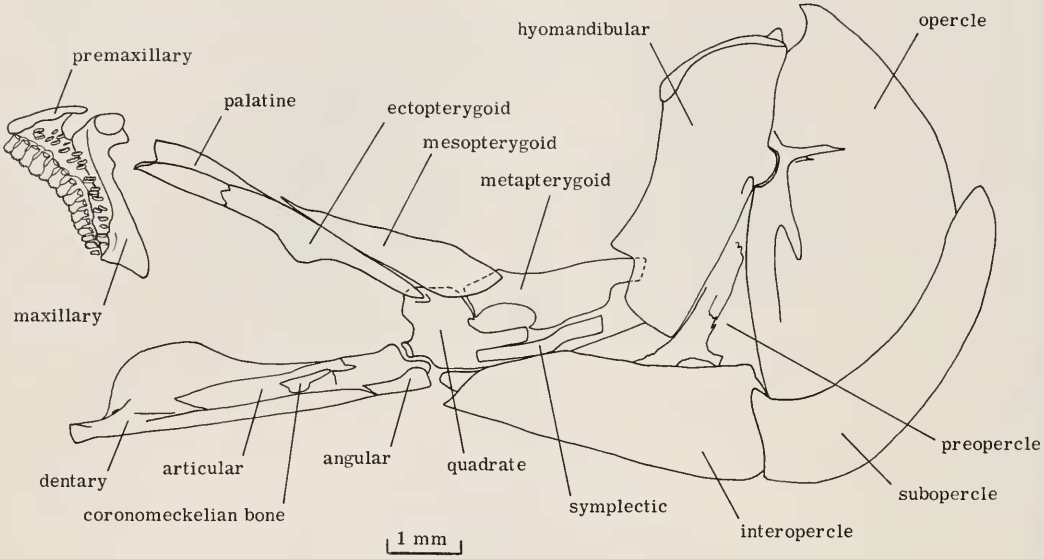

Figure 7. *Hemiodus semitaeniatus*, 55.8 mm. Jaws, suspensorium and opercular bones (medial view).

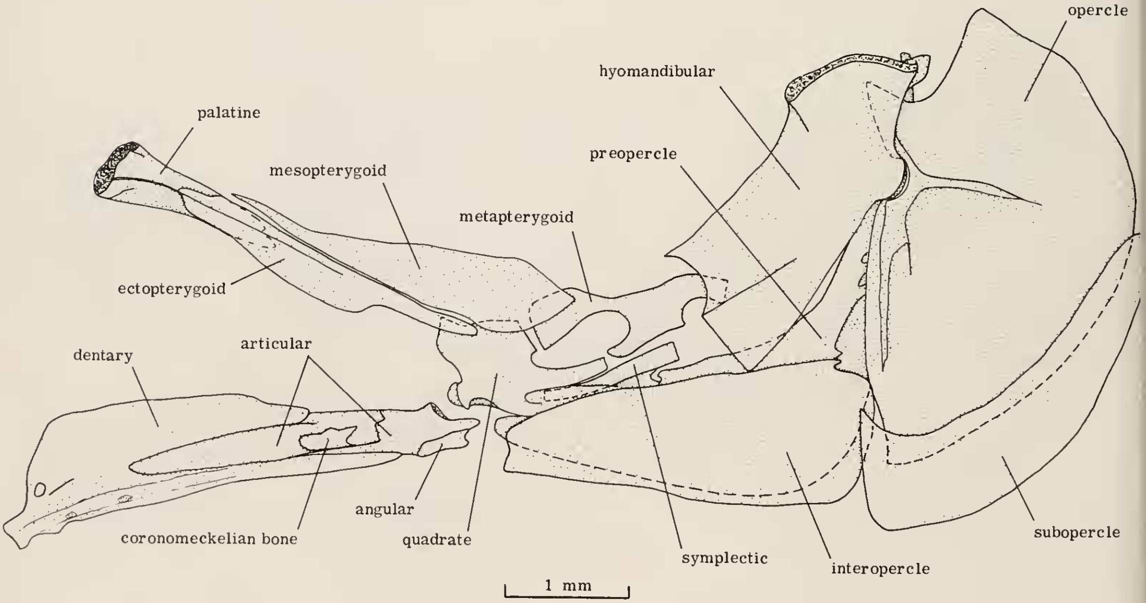

Figure 8. *Hemiodus quadrimaculatus*, 35.0 mm. Lower jaw, suspensorium and opercular bones (medial view).

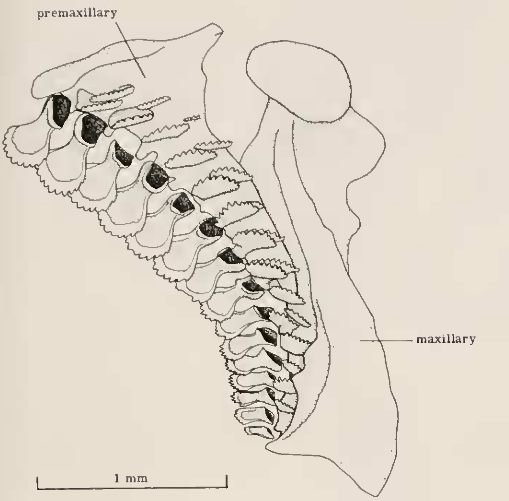

Figure 9. *Hemiodus semitaeniatus*, 55.8 mm. Upper jaw showing functional and replacement teeth (medial view).

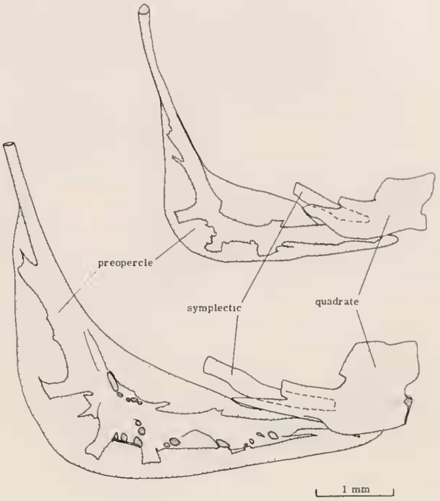

Figure 11. *Hemiodus*. Relationship of quadrate to preopercle (lateral view of bones from the right side). Upper: *H. quadrimaculatus*, 35.0 mm. Lower: *H. semitaeniatus*, 55.8 mm.

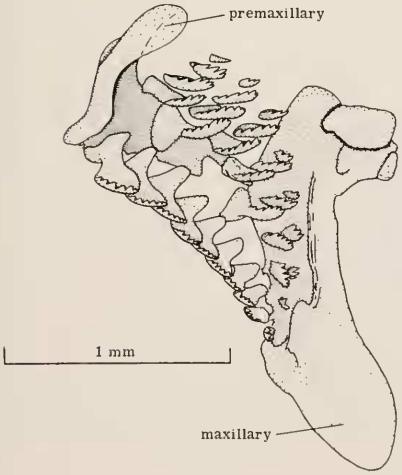

Figure 10. *Hemiodus quadrimaculatus*, 35.0 mm. Upper jaw showing functional and replacement teeth (medial view).

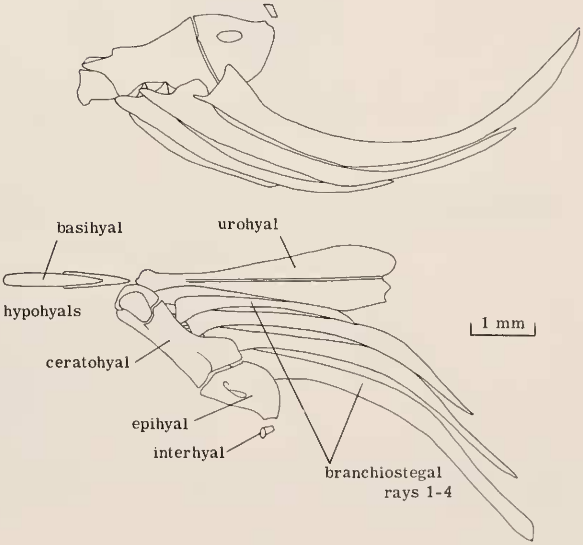

Figure 12. *Hemiodus semitaeniatus*, 55.8 mm. Upper: hyoid bar and branchiostegal rays (lateral view). Lower: hyoid arch and urohyal (dorsal view).

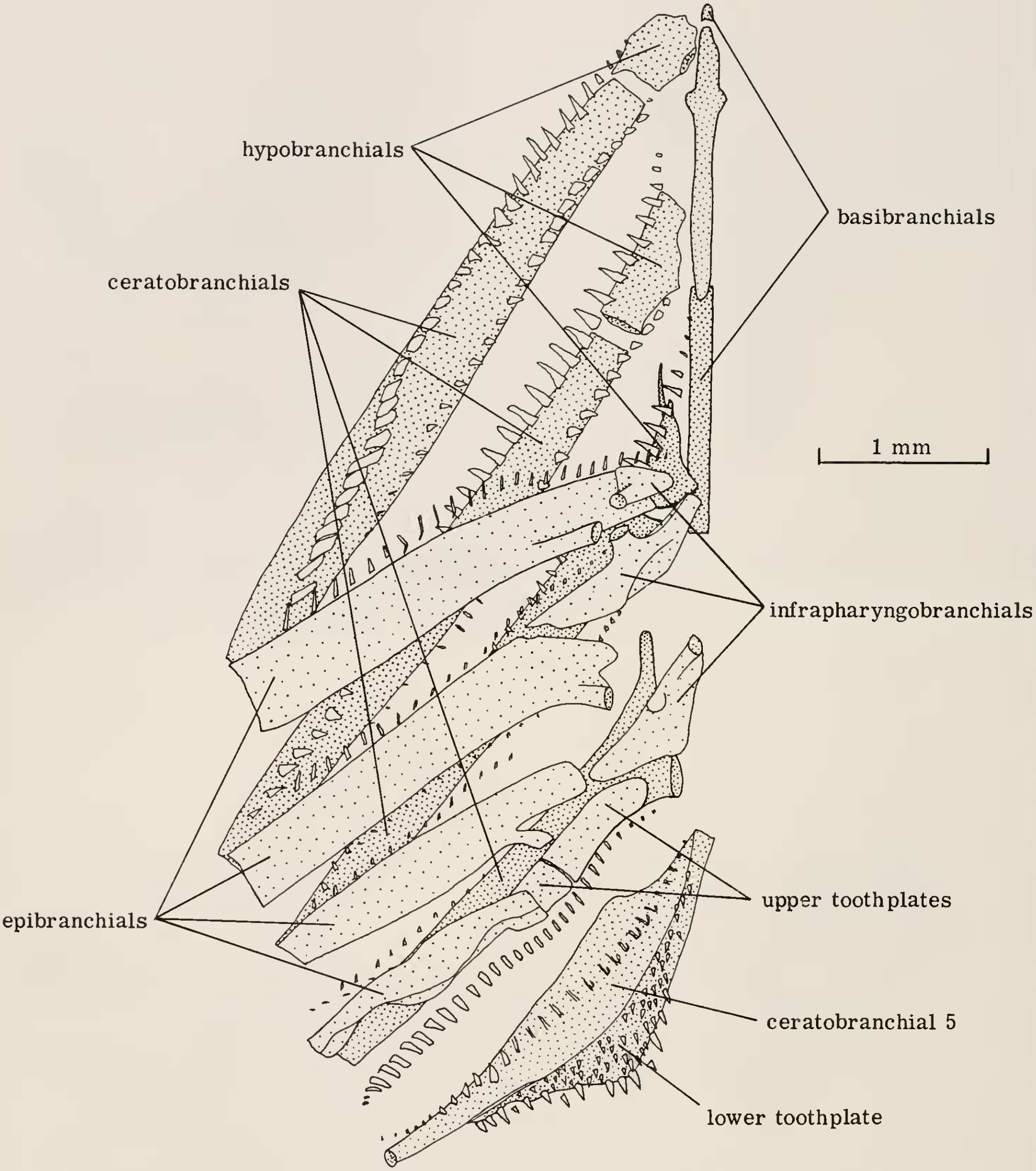

Figure 13. *Hemiodus semitaeniatus*, 55.8 mm. Branchial arches (dorsal view, with lateral elements of the right side removed).

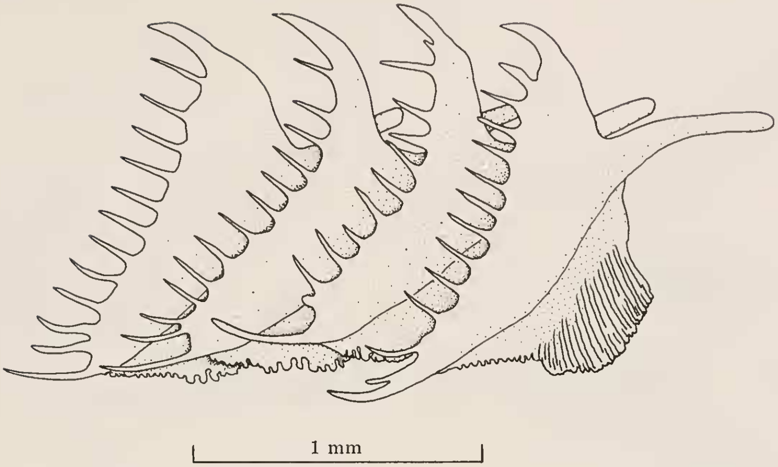

Figure 14. *Hemiodus microlepis*, 235 mm. Series of gill rakers from leading edge of ceratobranchial 1; rakers of trailing edge are nearly identical mirror images (dorsal view).

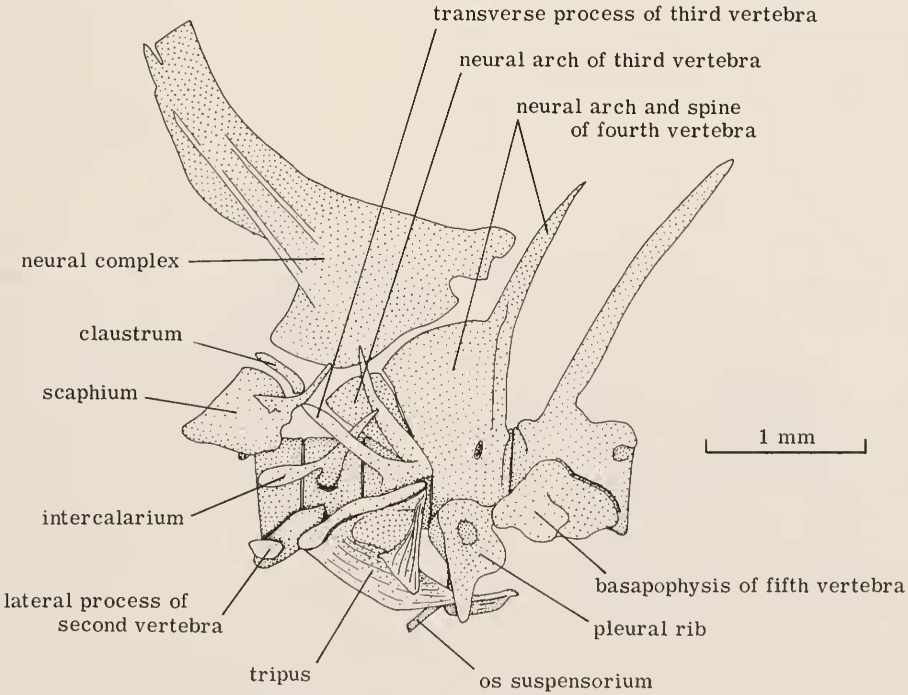
transverse process of third vertebra
neural arch of third vertebra
neural arch and spine of fourth vertebra
neural complex
claustrum
scaphium
1 mm
intercalarium
basapophysis of fifth vertebra
lateral process of second vertebra
pleural rib
tripus
os suspensorium

Figure 15. *Hemiodus semitaeniatus*, 55.8 mm. Weberian apparatus (lateral view).

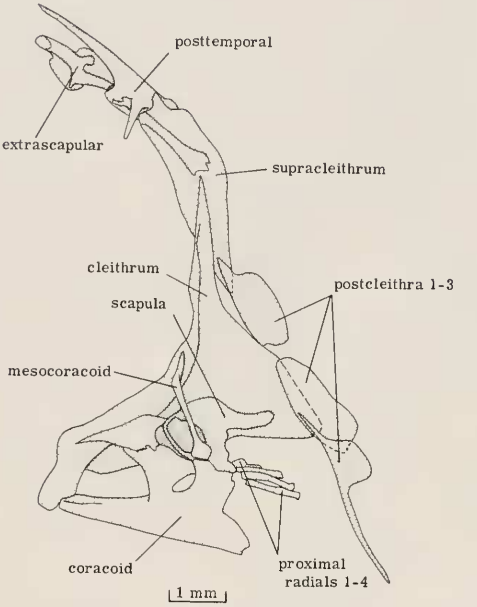

Figure 16. *Hemiodus semitaeniatus*, 55.8 mm. Right half of pectoral girdle (medial view).

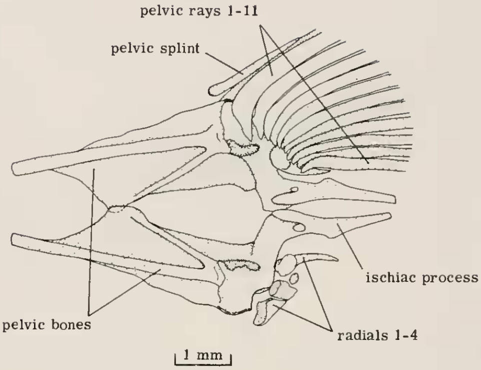

Figure 17. *Hemiodus semitaeniatus*, 55.8 mm. Pelvic girdle (ventral view).

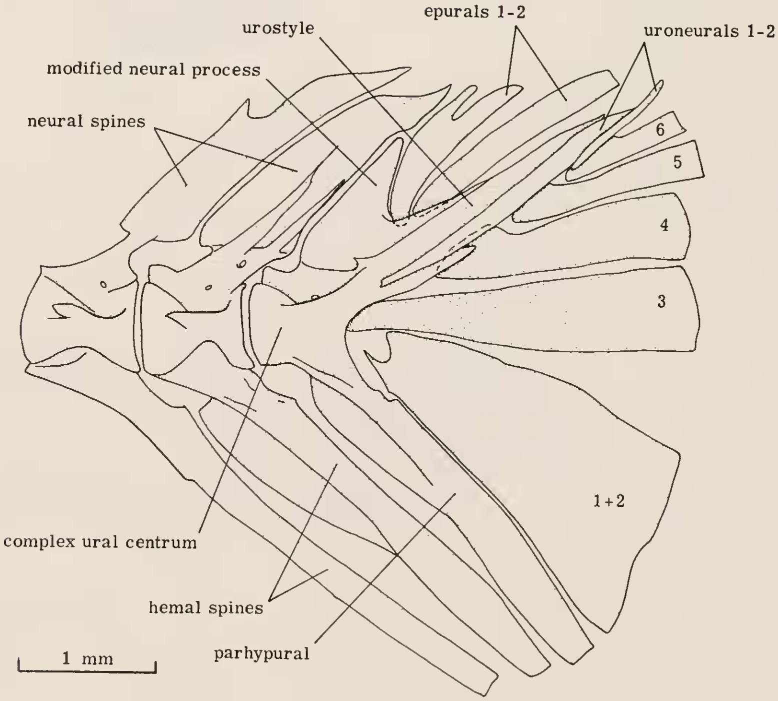

Figure 18. *Hemiodus semitaeniatus*, 54.4 mm. Caudal skeleton (lateral view).

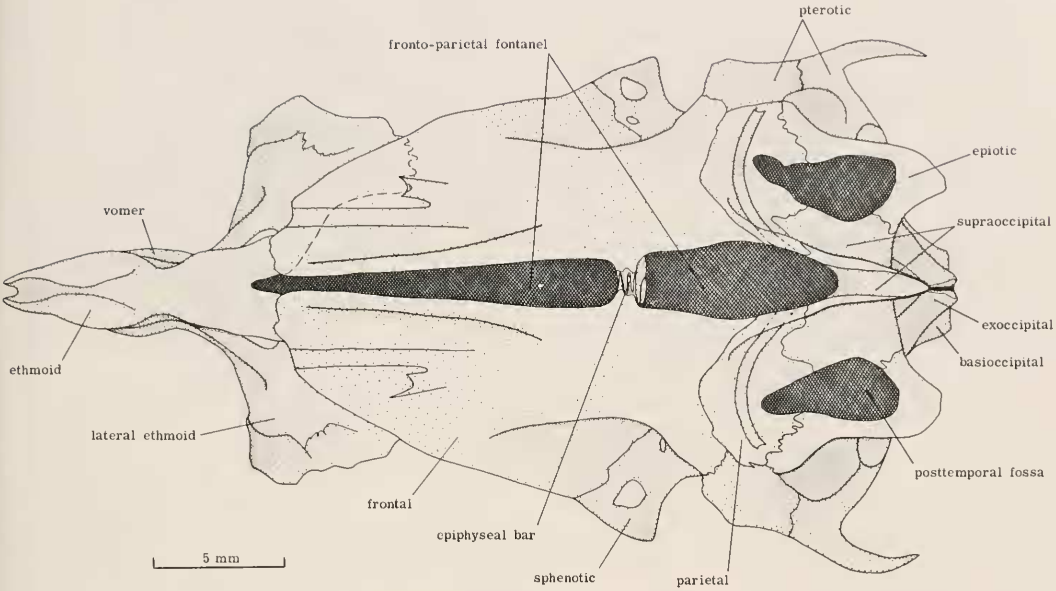

Figure 19. *Argonectes longiceps*, 198 mm. Cranium (dorsal view).

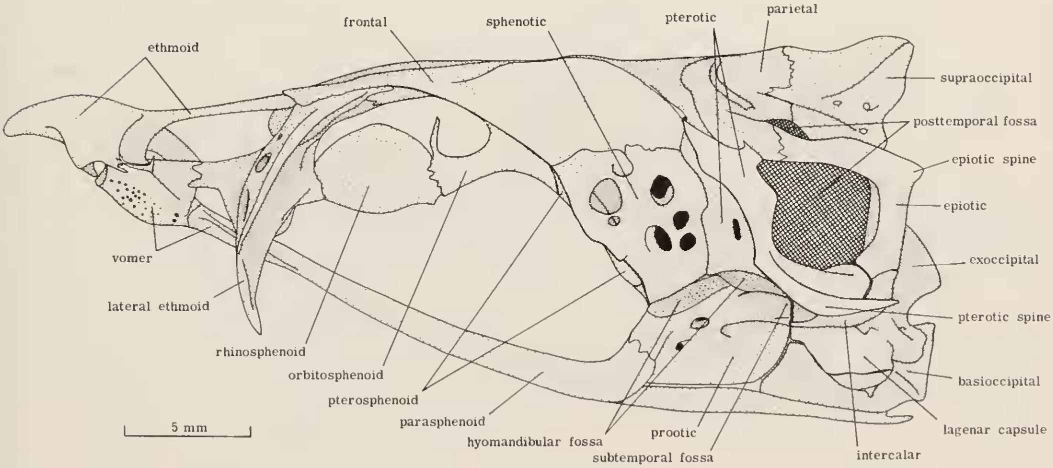

Figure 20. *Argonectes longiceps*, 198 mm. Cranium (lateral view).

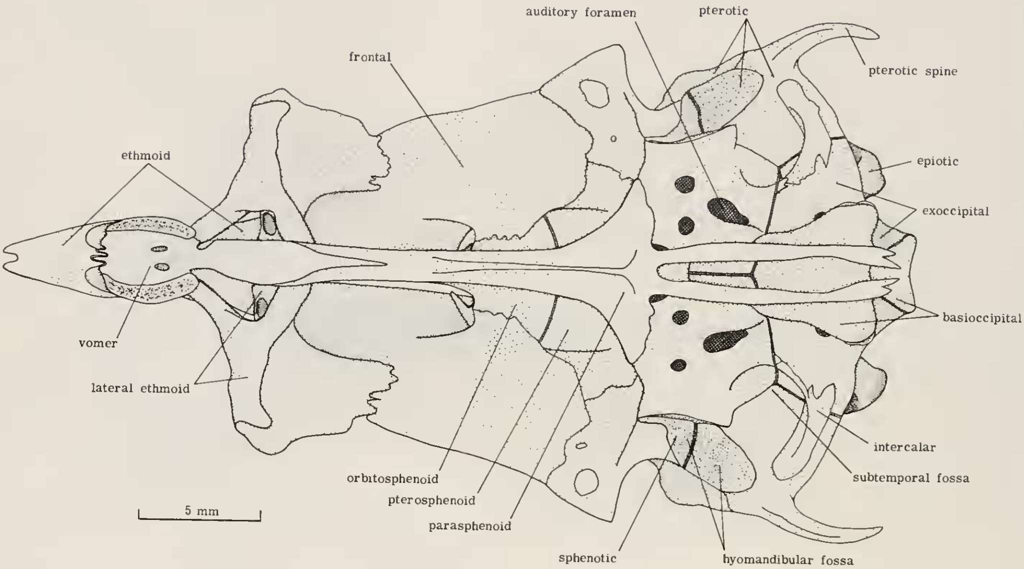

Figure 21. *Argonectes longiceps*, 198 mm. Cranium (ventral view).

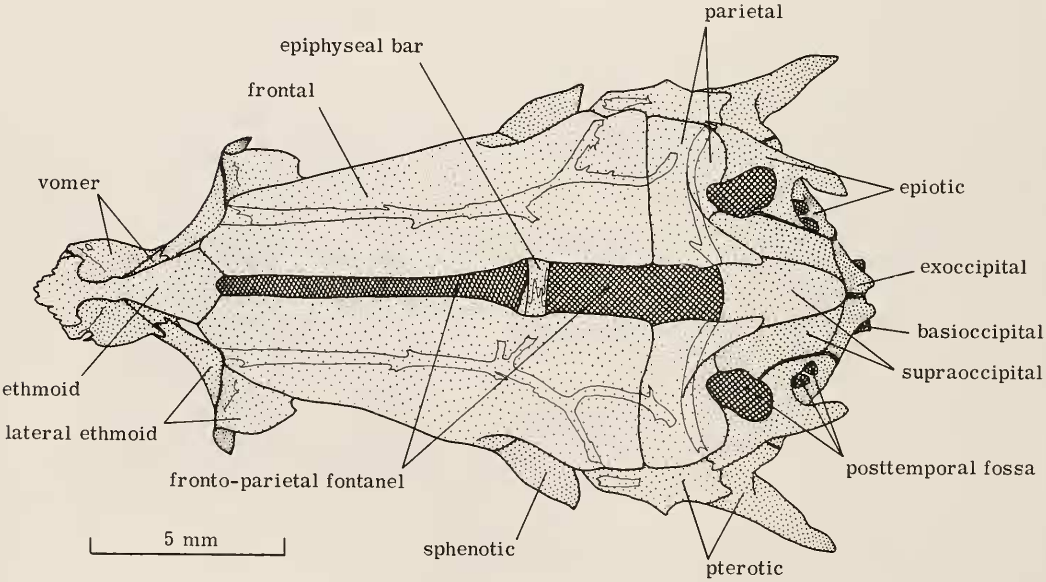

Figure 22. *Bivibranchia protractila*, 115.2 mm. Cranium (dorsal view).

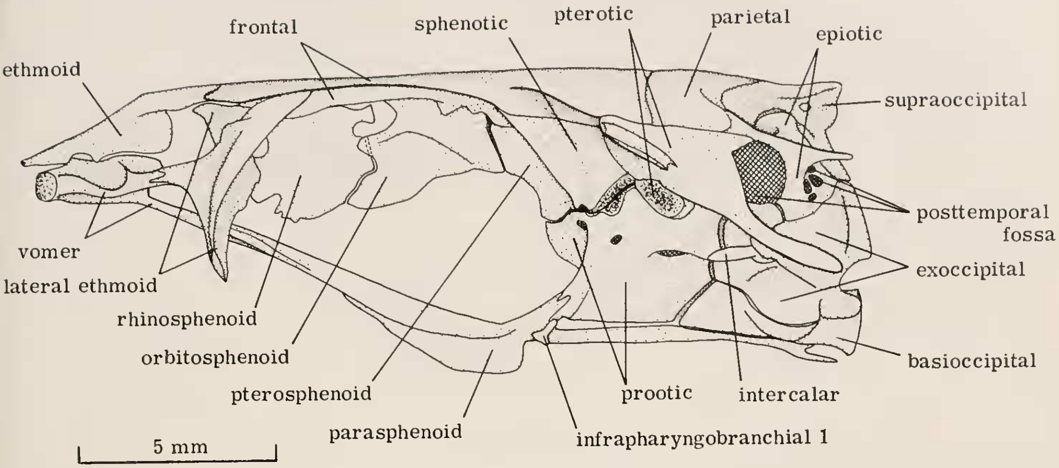

Figure 23. *Bivibranchia protractila*, 115.2 mm. Cranium (lateral view).

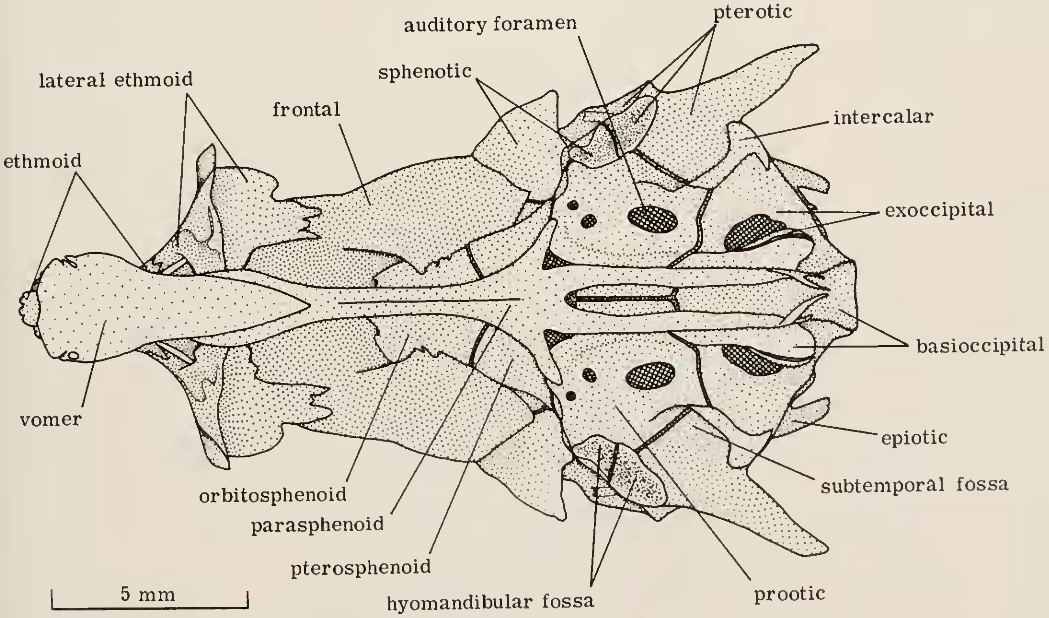

Figure 24. *Bivibranchia protractila*, 115.2 mm. Cranium (ventral view).

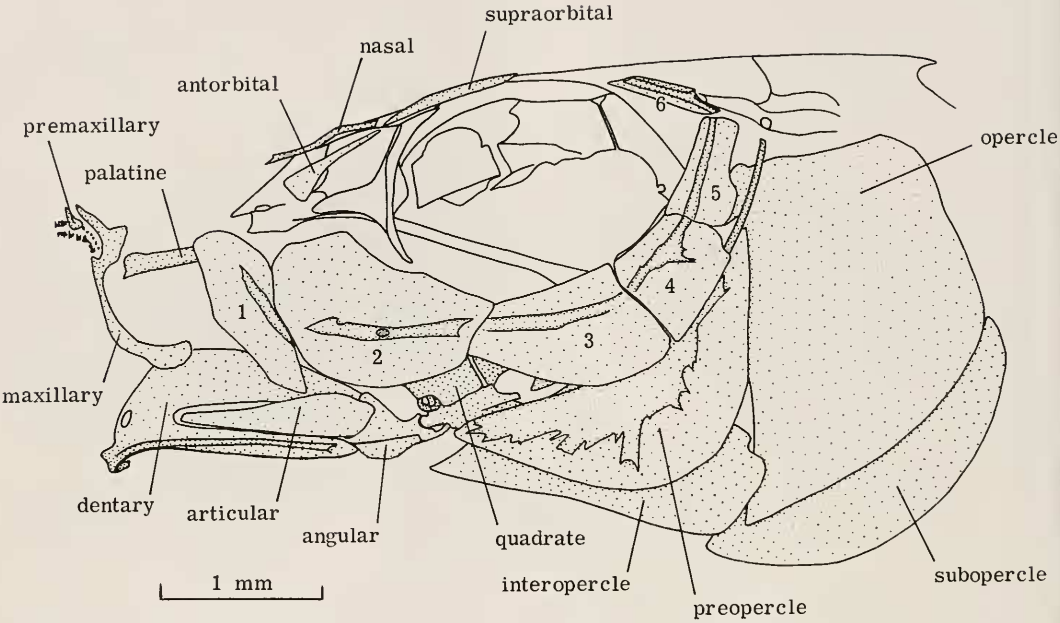

Figure 25. *Bivibranchia protractila*, 39.9 mm. Lateral bones of skull (lateral view) (upper jaw of specimen slightly damaged).

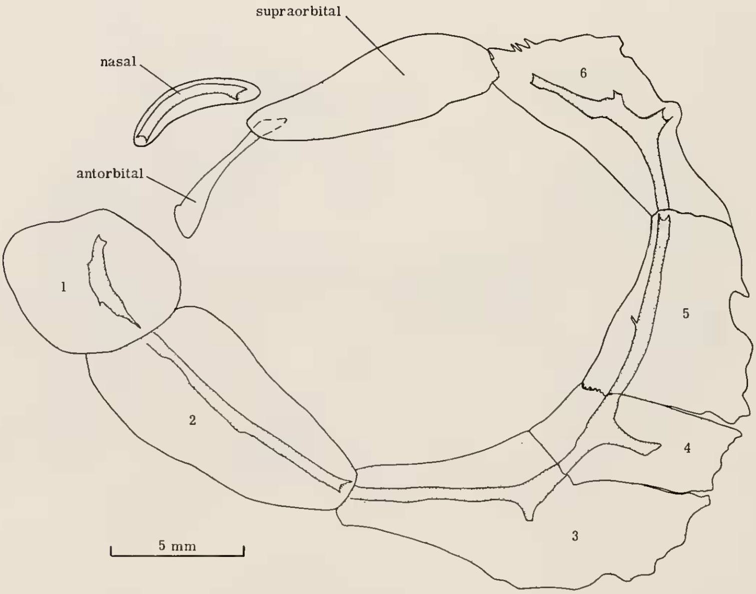

Figure 26. *Argonectes longiceps*, 198 mm. Nasal, antorbital and circumorbital bones (lateral view).

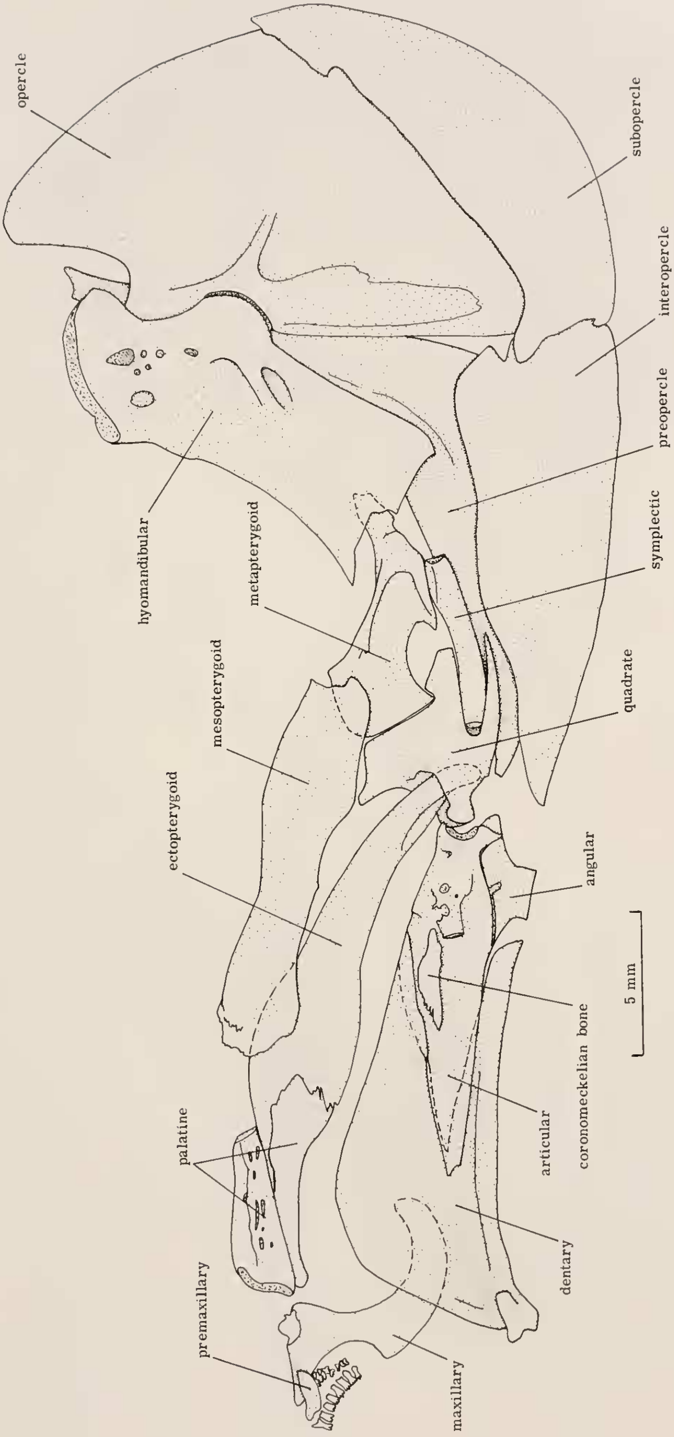

Figure 27. *Argonectes longiceps*, 198 mm. Jaws, suspensorium and opercular bones (medial view).

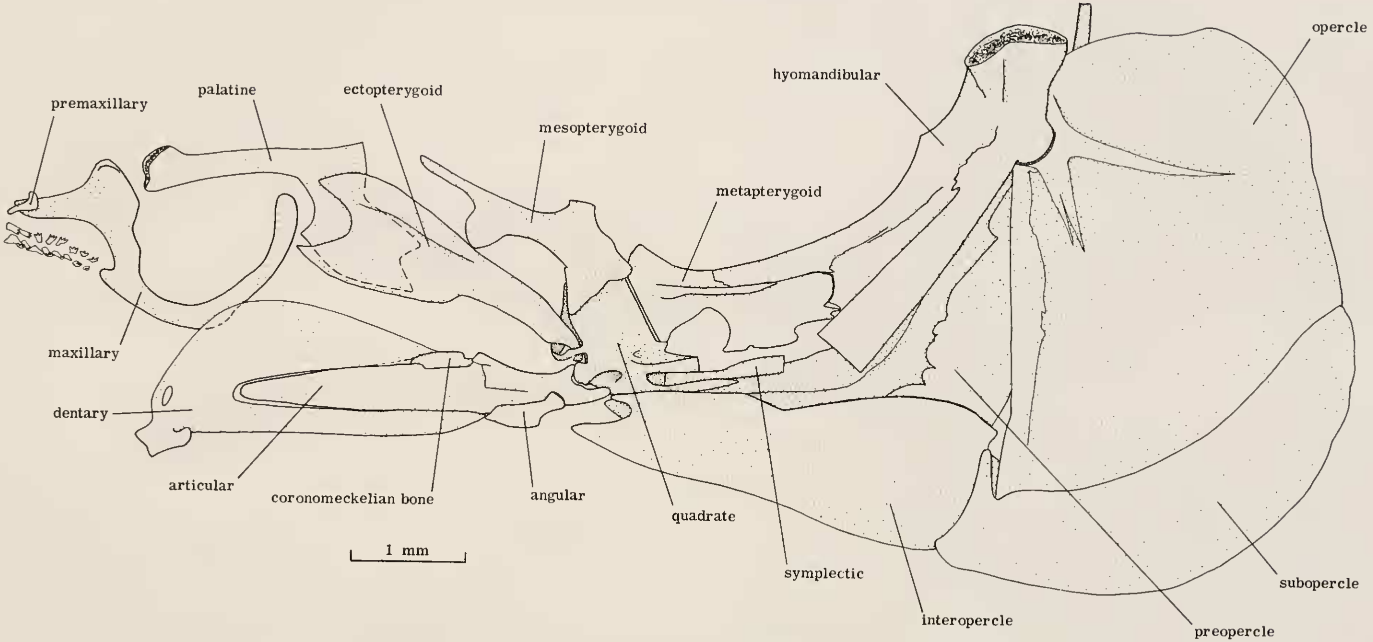

Figure 28. *Bivibranchia protractila*, 39.9 mm. Jaws, suspensorium and opercular bones (medial view) (upper jaw based on 115.2-mm specimen).

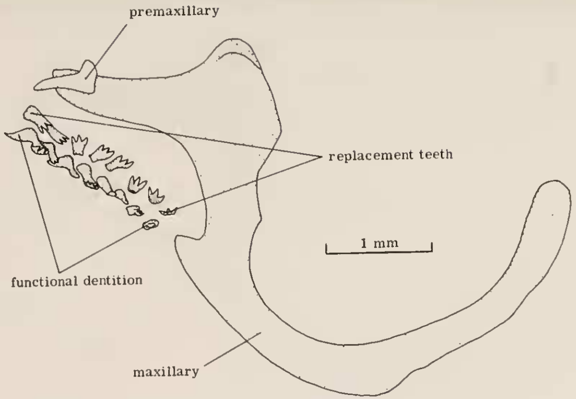

Figure 29. *Bivibranchia protractila*, 115.2 mm. Upper jaw showing functional and replacement teeth (medial view).

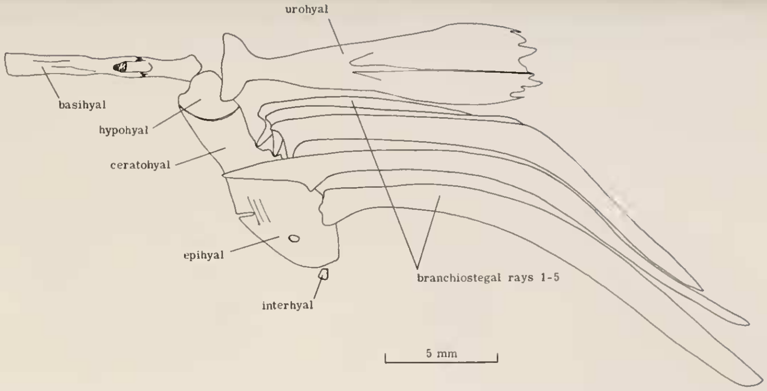

Figure 30. *Argonectes longiceps*, 198 mm. Hyoid arch and urohyal bone (ventral view).

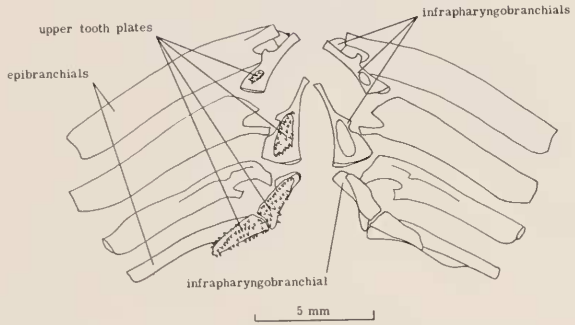

Figure 31. *Argonectes longiceps*, 198 mm. Upper half of branchial arches (ventral view) (gill rakers removed).

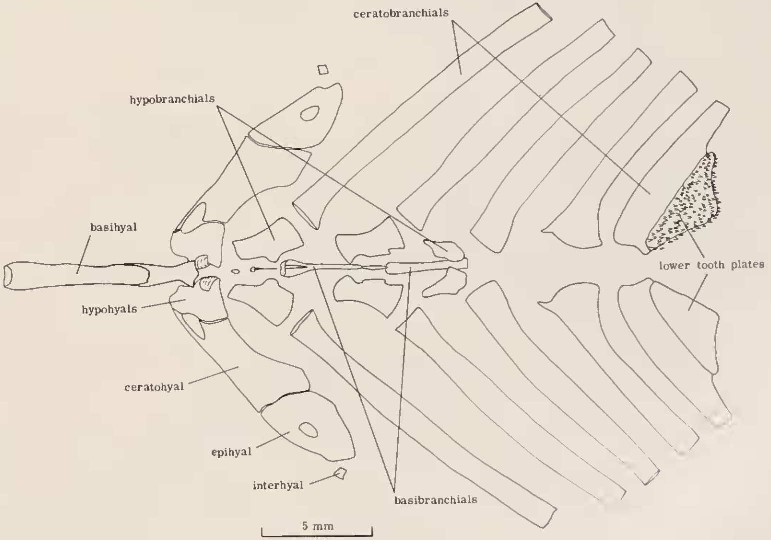

Figure 32. *Argonectes longiceps*, 198 mm. Lower half of branchial arches (dorsal view) (gill rakers removed).

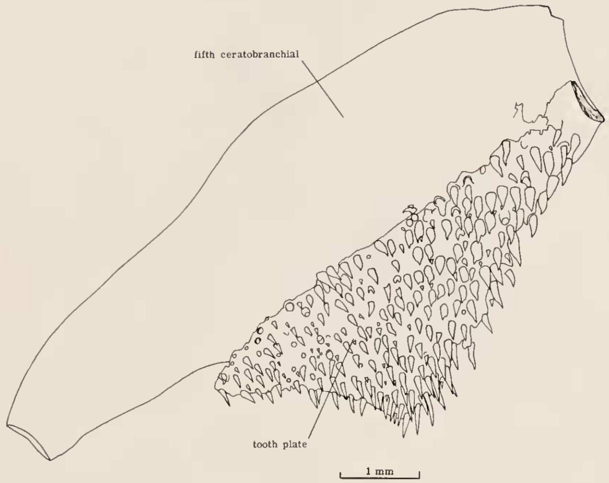

Figure 33. *Argonectes longiceps*, 198 mm. Fifth ceratobranchial and lower pharyngeal toothplate of left side (dorsal view).

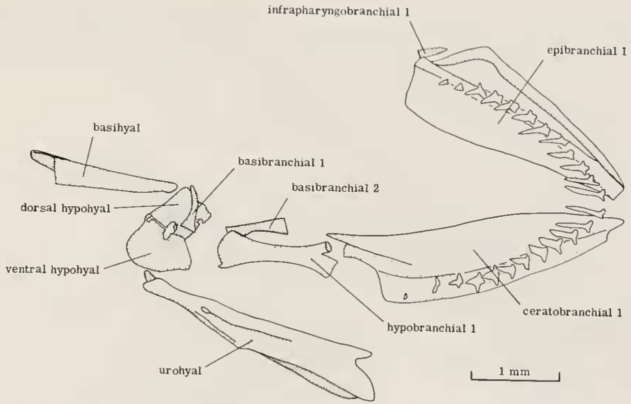

Figure 34. *Bivibranchia protractila*, 39.9 mm. Portions of hyoid arch and first two branchial arches (lateral view) (hypohyals of left side removed).

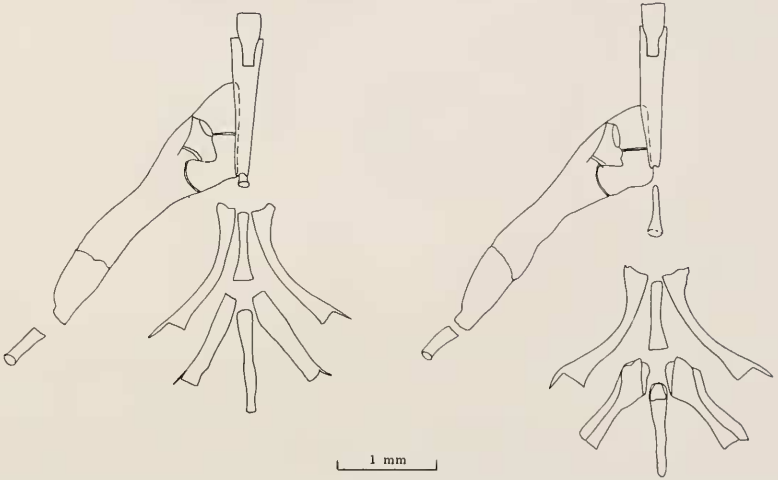

Figure 35. *Bivibranchia protractila*, 39.9 mm. Portion of hyoid arch and first two branchial arches to show possible pivotal movement of basibranchial 1. Left, contraction. Right, expansion (dorsal view).

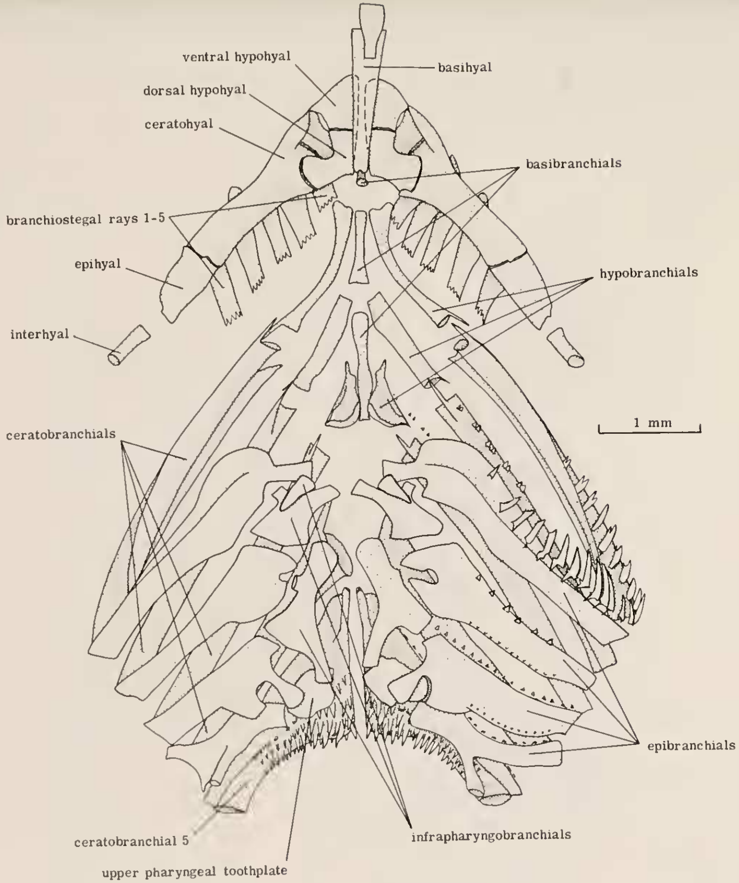

Figure 36. *Bivibranchia protractila*, 39.9 mm. Hyoid and branchial arches (dorsal view).

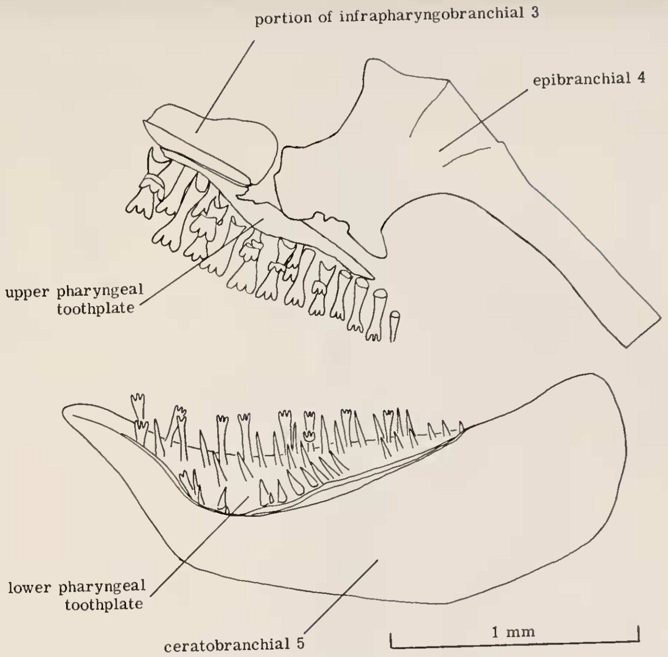
portion of infrapharyngobranchial 3
epibranchial 4
upper pharyngeal toothplate
lower pharyngeal toothplate
ceratobranchial 5
1 mm

Figure 37. *Bivibranchia protractila*, 39.9 mm. Ceratobranchial 5, epibranchial 4, portion of infrapharyngobranchial 3 and associated upper and lower pharyngeal toothplates of the right side (slightly oblique posterior view).

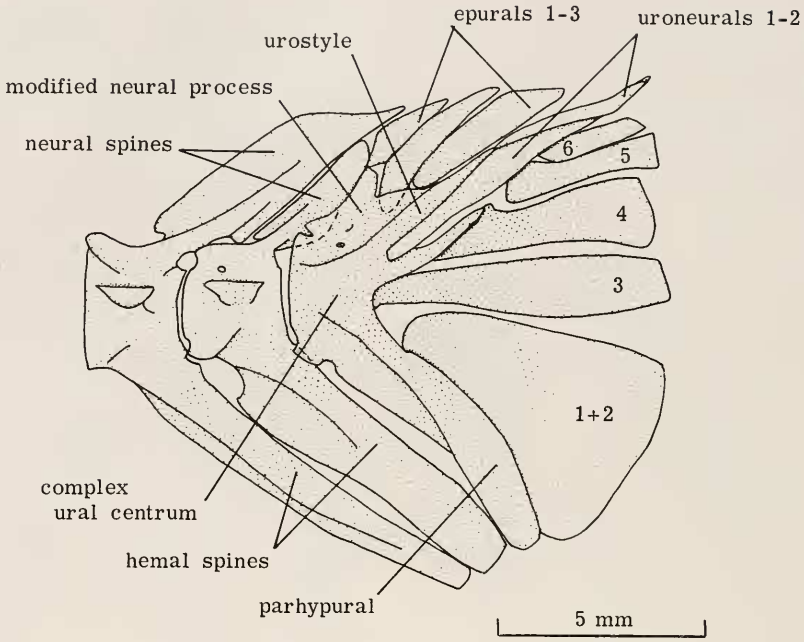

Figure 38. *Argonectes longiceps*, 198 mm. Caudal skeleton (lateral view).

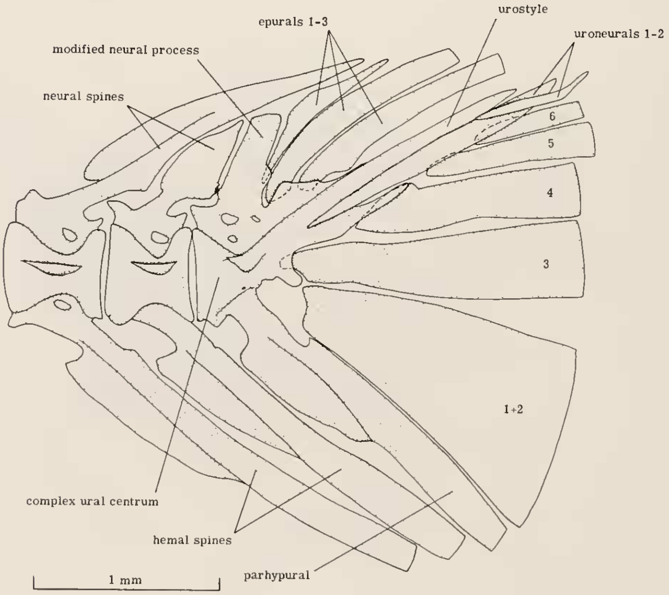

Figure 39. *Bivibranchia protractila*, 39.9 mm. Caudal skeleton (lateral view).

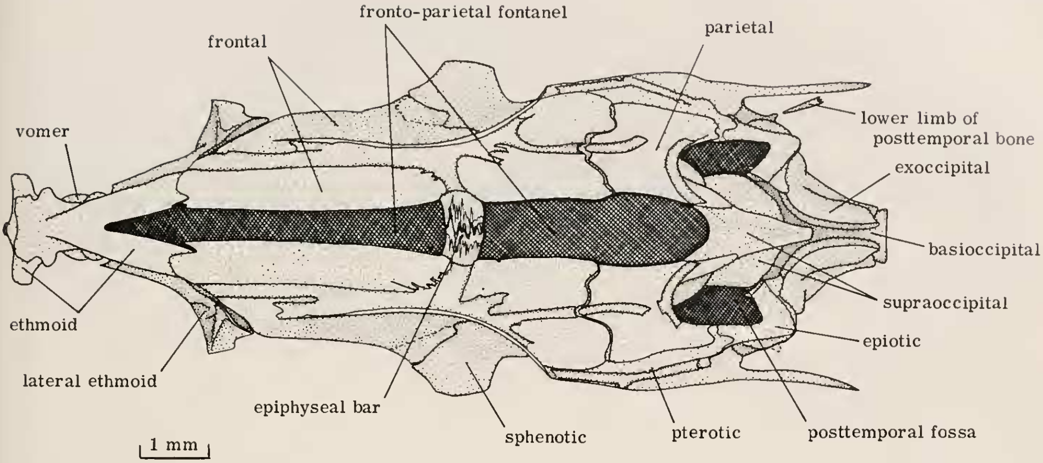

Figure 40. *Anodus melanopogon*, 55.0 mm. Cranium (dorsal view).

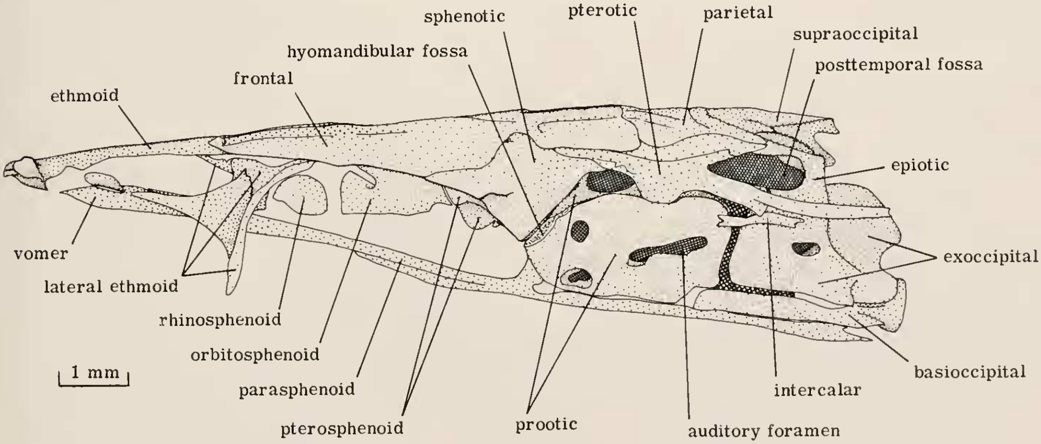

Figure 41. *Anodus melanopogon*, 55.0 mm. Cranium (lateral view).

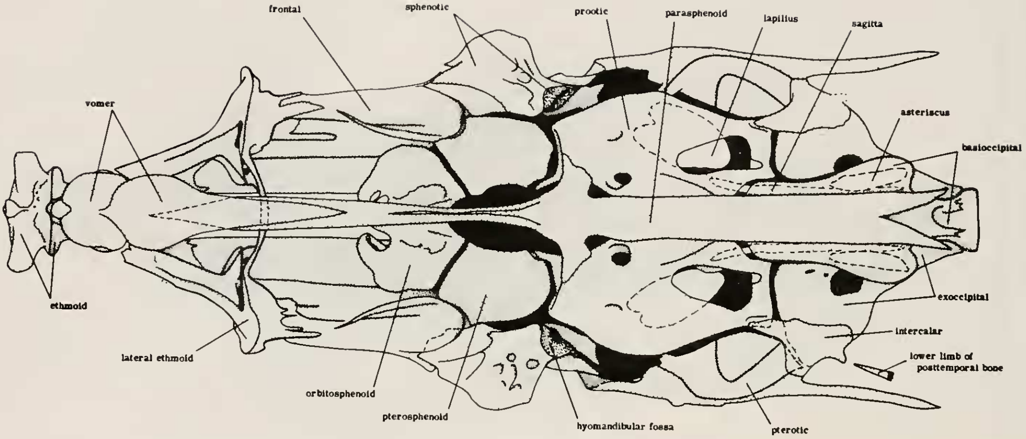

Figure 42. *Anodus melanopogon*, 55.0 mm. Cranium (ventral view).

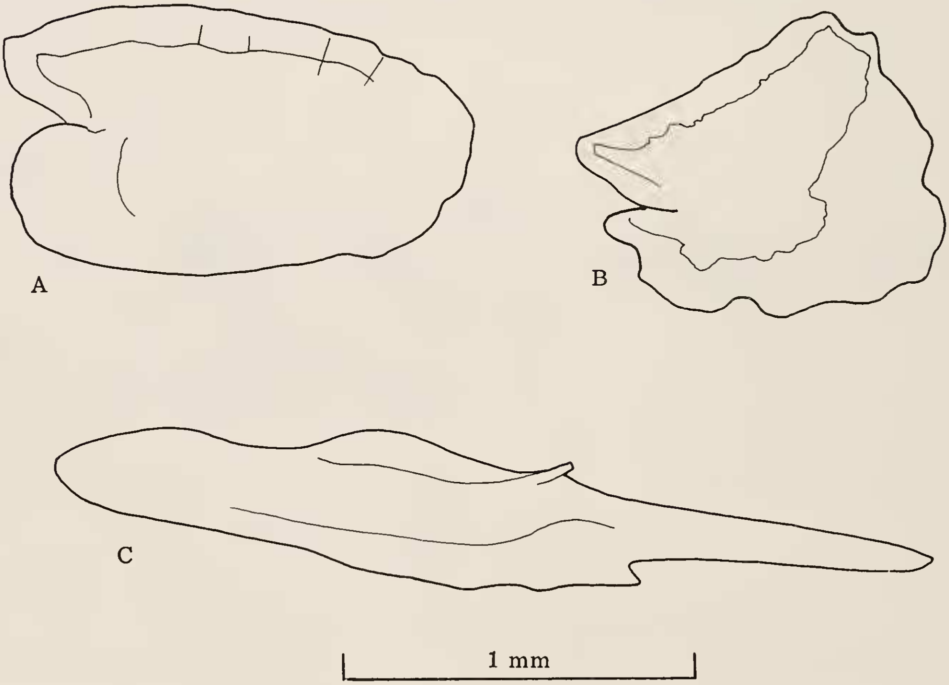

Figure 43. *Anodus melanopogon*, 55.5 mm. Otoliths of left side. A. Lapillus (ventral view). B. Asteriscus (lateral view). C. Sagitta (lateral view).

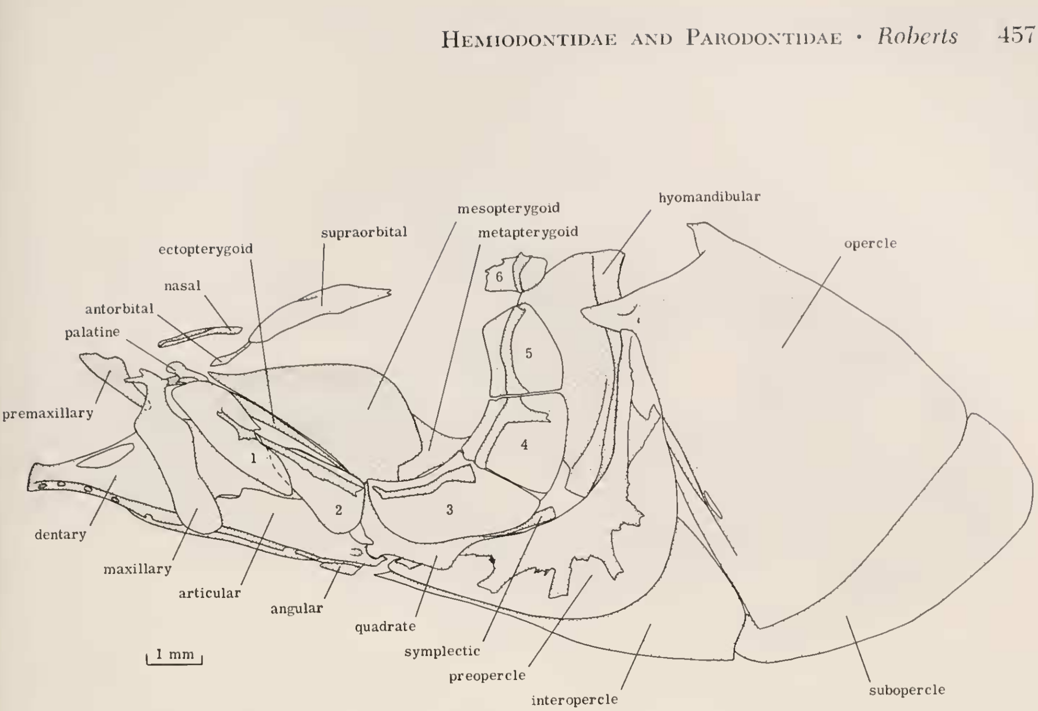

Figure 44. *Anodus melanopogon*, 55.0 mm. Lateral bones of skull (lateral view).

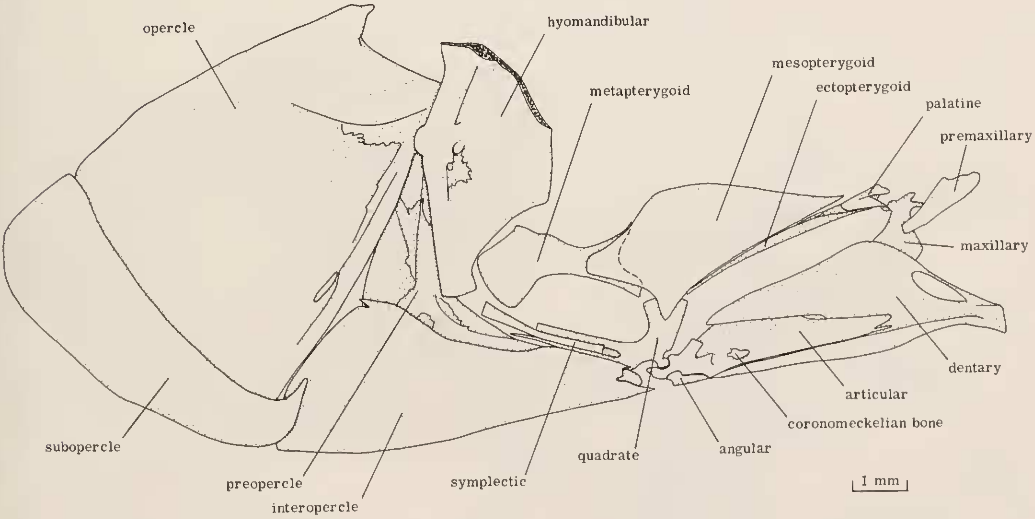

Figure 45. *Anodus melanopogon*, 55.0 mm. Jaws, suspensorium and opercular bones (medial view).

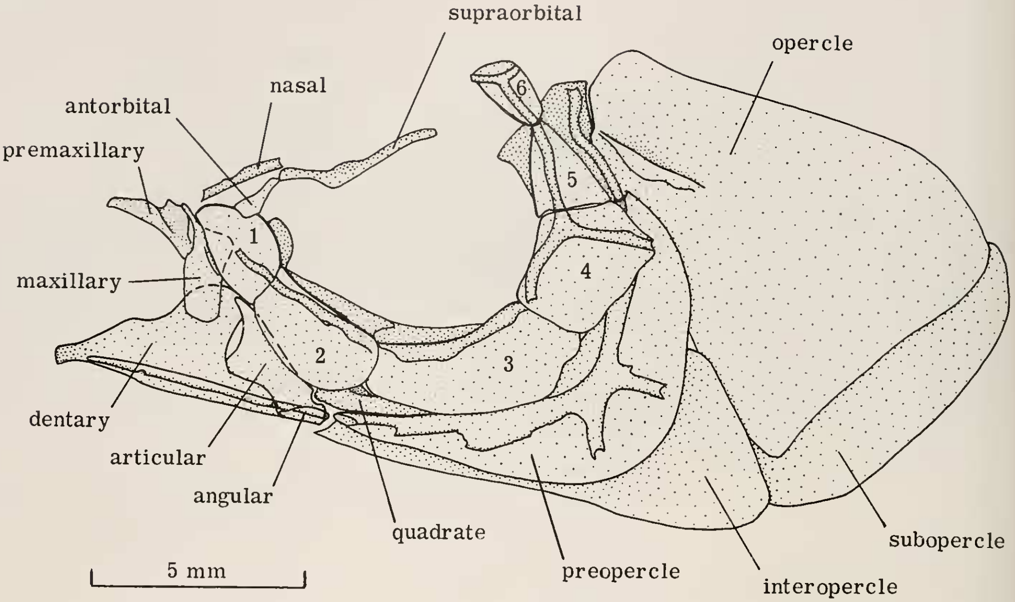

Figure 46. *Gasterotomus latior*, 76.7 mm. Lateral bones of skull (lateral view).

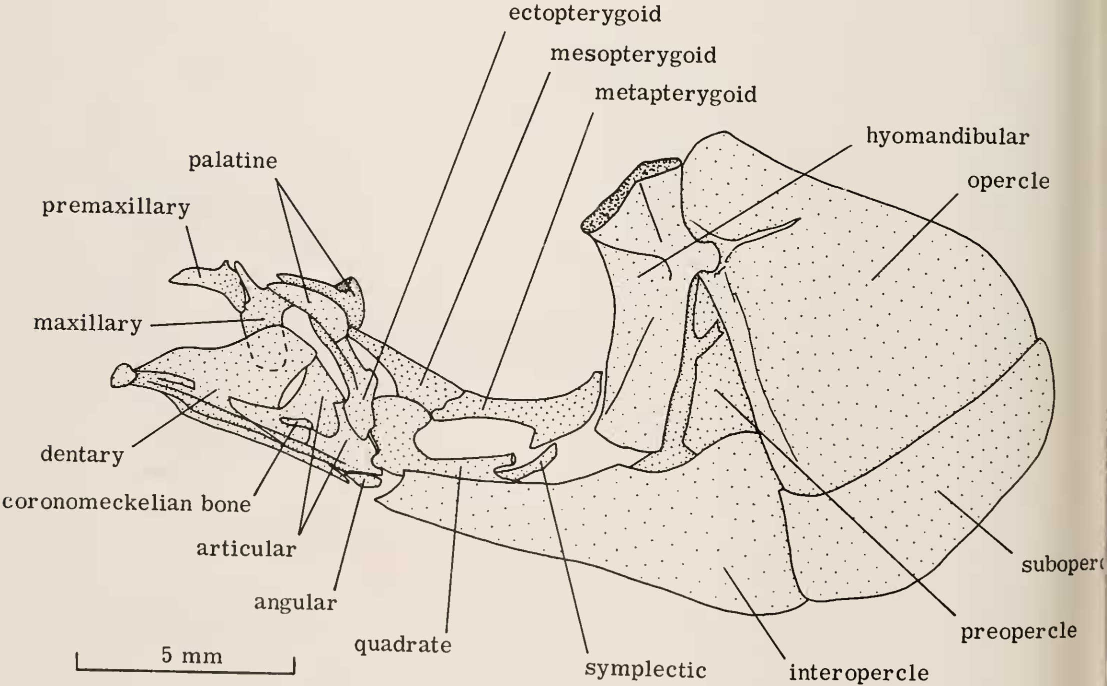

Figure 47. *Gasterotomus latior*, 76.7 mm. Jaws, suspensorium and opercular bones (medial view).

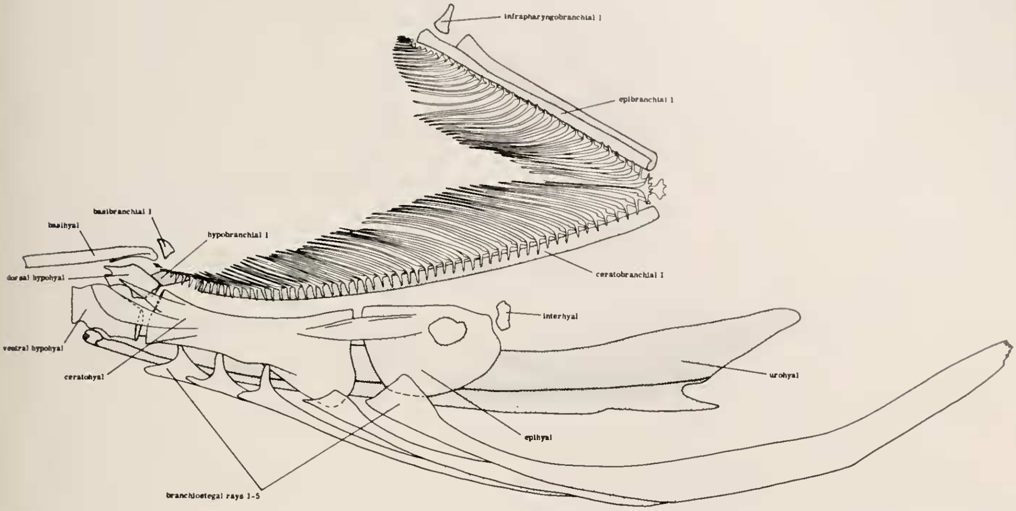

Figure 48. *Anodus melanopogon*, 55.0 mm. Hyoid arch, urohyal bone and first branchial arch (lateral view).

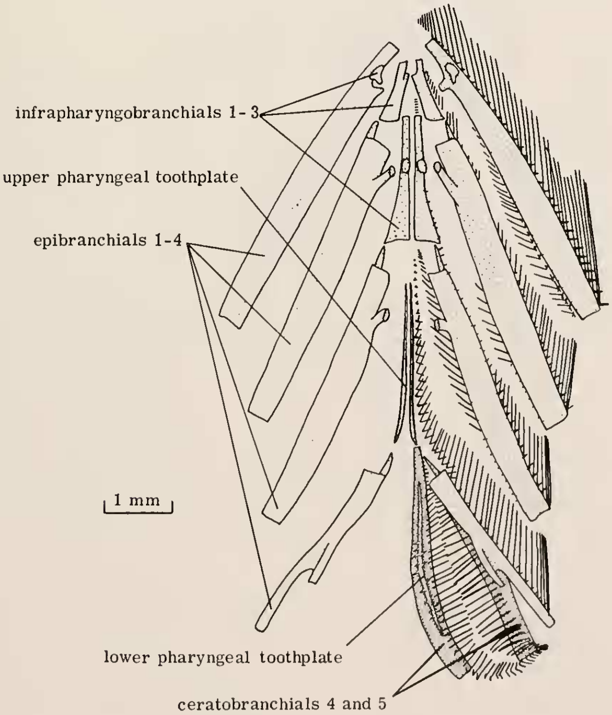
infrapharyngobranchials 1-3
upper pharyngeal toothplate
epibranchials 1-4
1 mm
lower pharyngeal toothplate
ceratobranchials 4 and 5

Figure 49. *Anodus melanopogon*, 55.0 mm. Upper half of branchial arches (dorsal view).

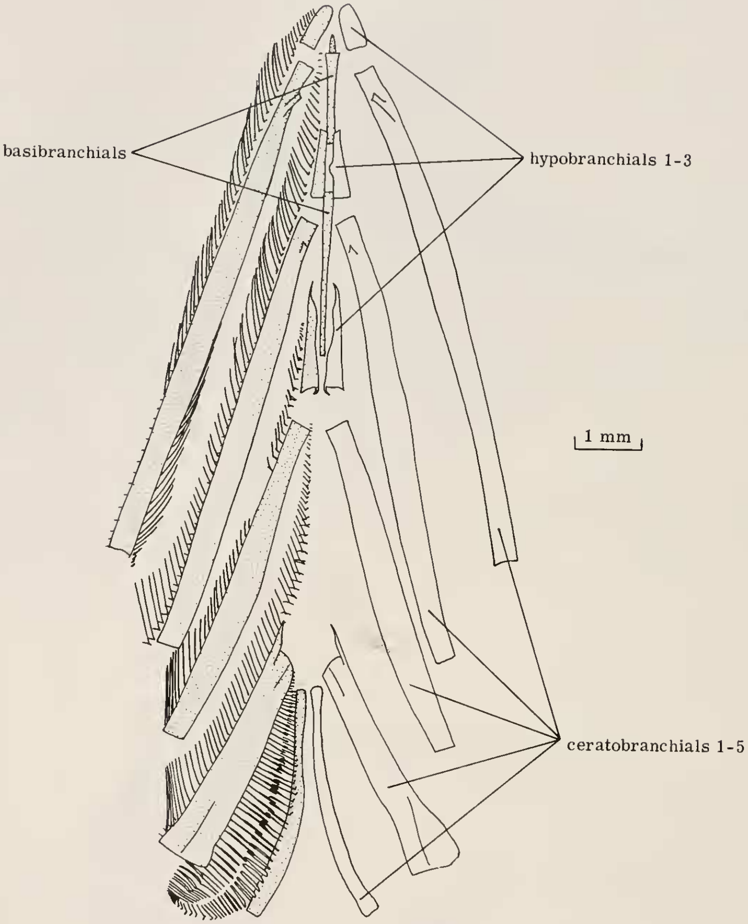

Figure 50. *Anodus melanopogon*, 55.0 mm. Lower half of branchial arches (dorsal view).

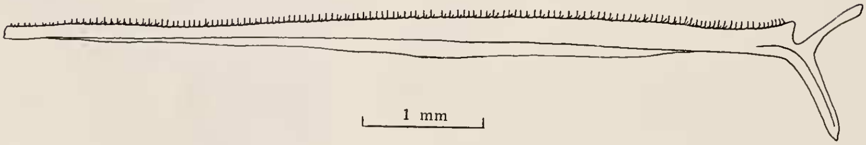

Figure 51. *Anodus elongatus*, 180 mm. Gill raker from leading edge of ceratobranchial 1 showing ctenii.

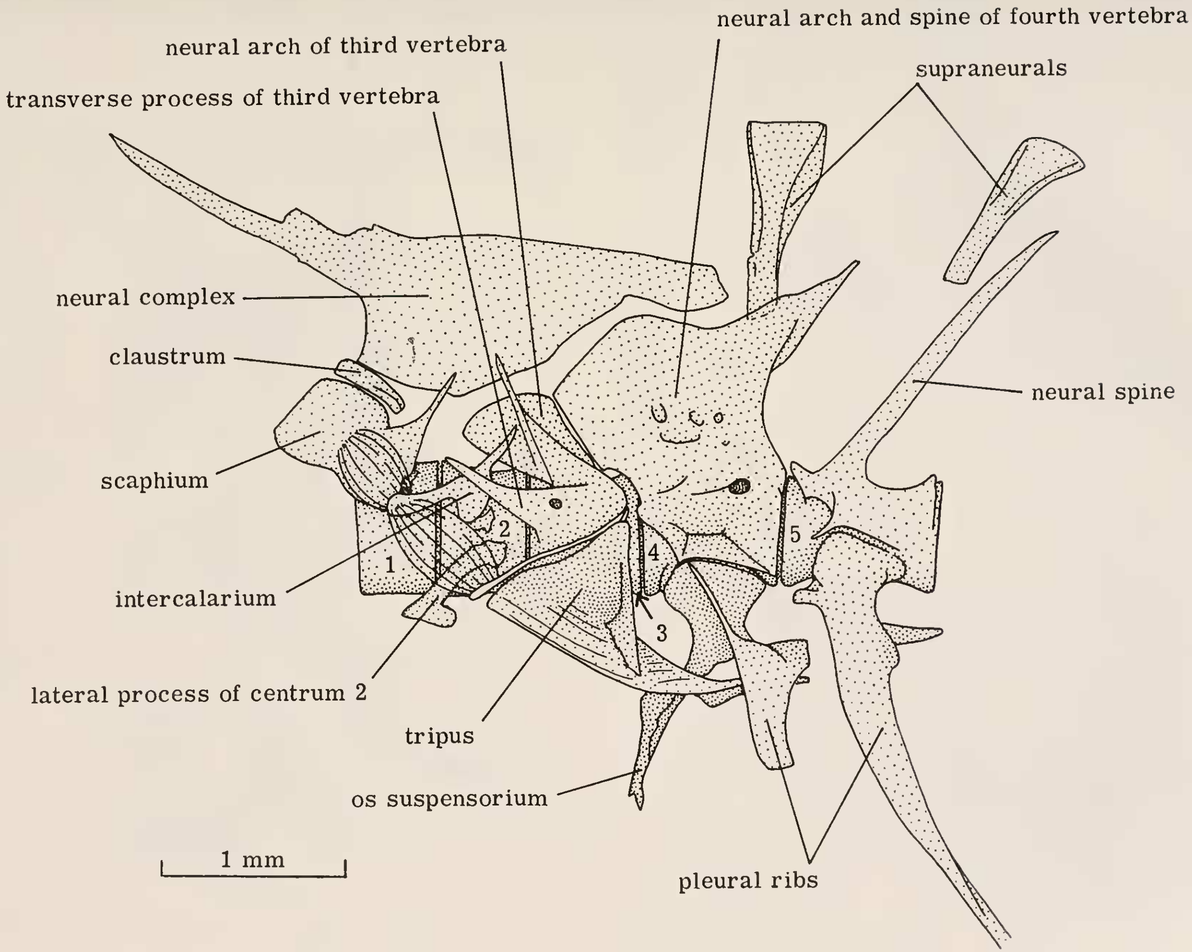
neural arch and spine of fourth vertebra
neural arch of third vertebra
supraneurals
transverse process of third vertebra
neural complex
claustrum
neural spine
scaphium
5
2
4
1
intercalarium
3
lateral process of centrum 2
tripus
os suspensorium
1 mm
pleural ribs

Figure 52. *Anodus melanopogon*, 55.0 mm. Weberian apparatus (lateral view).

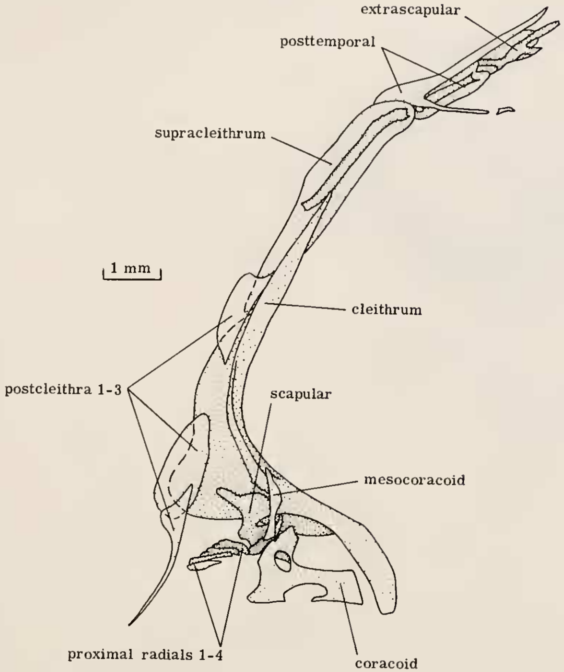

Figure 53. *Anodus melanopogon*, 55.0 mm. Left half of pectoral girdle (medial view).

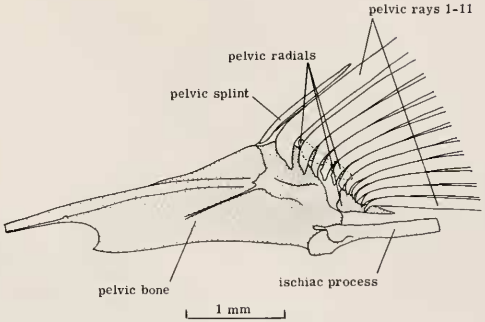

Figure 54. *Anodus melanopogon*, 55.0 mm. Left half of pelvic girdle (ventral view).

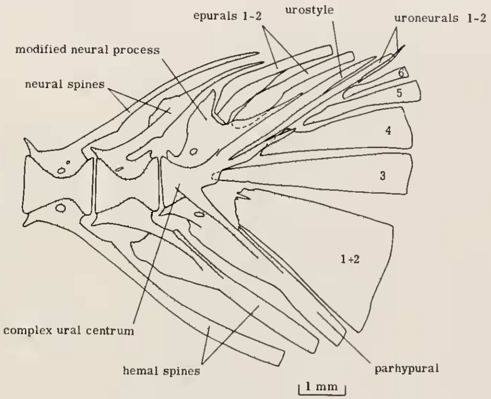

Figure 55. *Anodus melanopogon*, 55.0 mm. Caudal skeleton (lateral view).

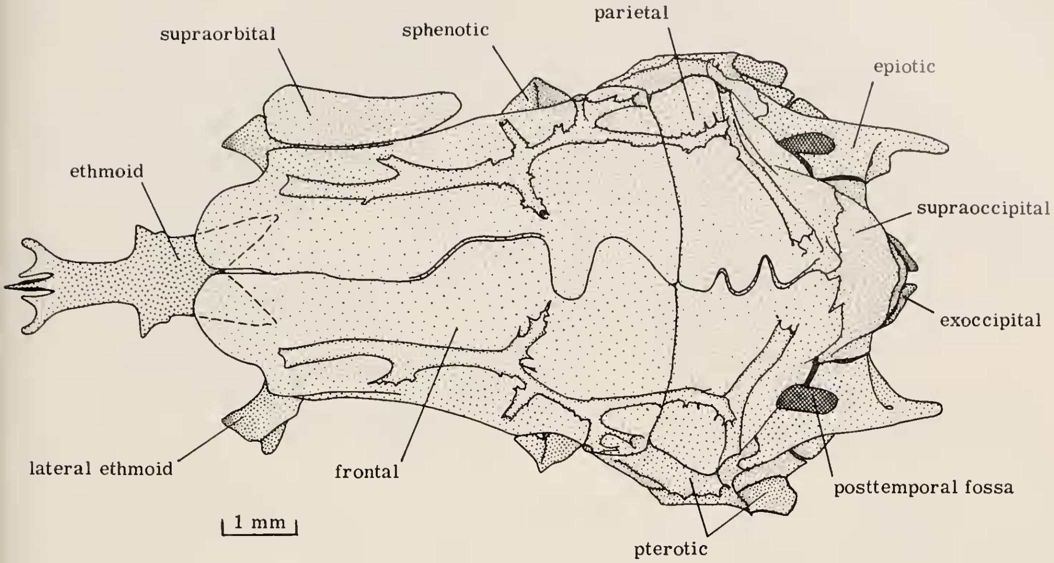

Figure 56. *Saccodon wagneri* (dental morph IV), 55.4 mm. Cranium with right supraorbital in place (dorsal view).

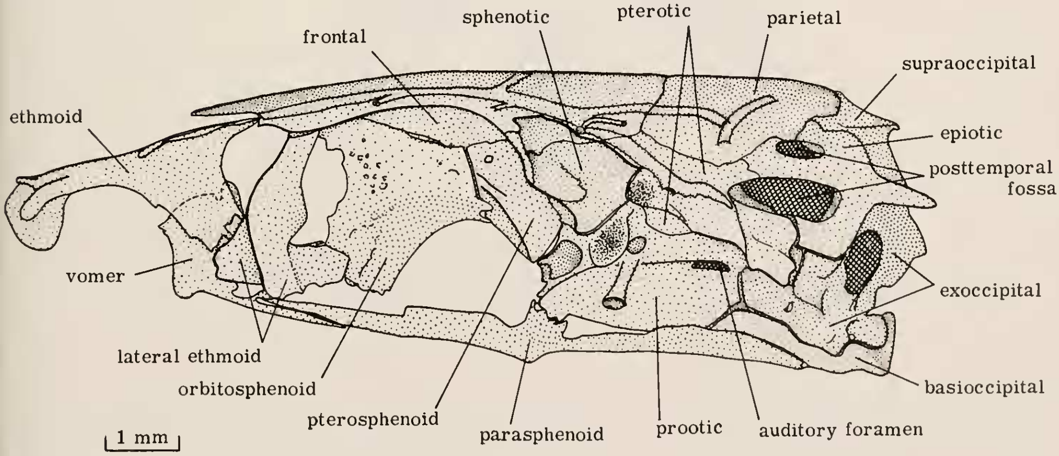

Figure 57. *Saccodon wagneri* (dental morph IV), 55.4 mm. Cranium (lateral view).

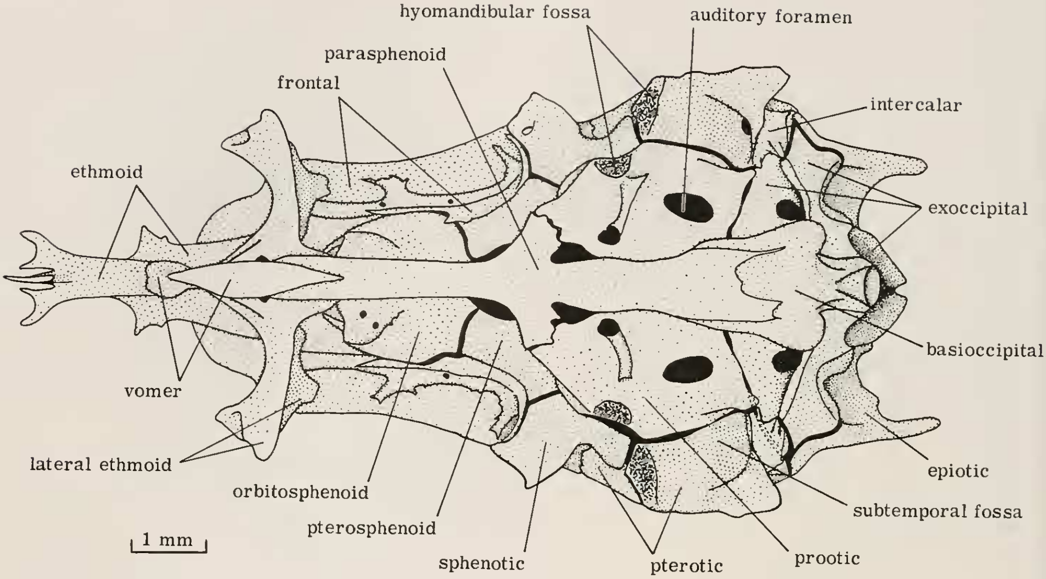

Figure 58. *Saccodon wagneri* (dental morph IV), 55.4 mm. Cranium (ventral view).

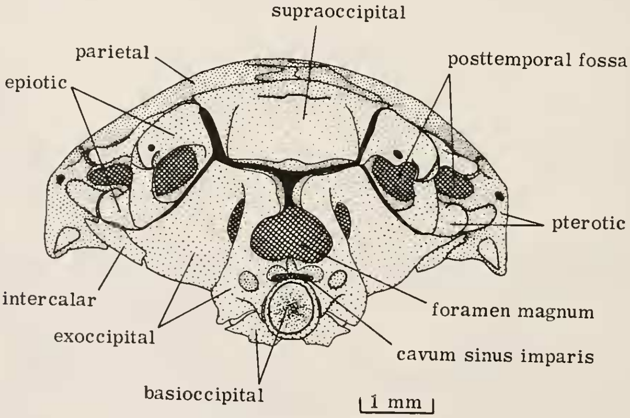

Figure 59. *Saccodon wagneri* (dental morph IV), 55.4 mm. Cranium (occipital view).

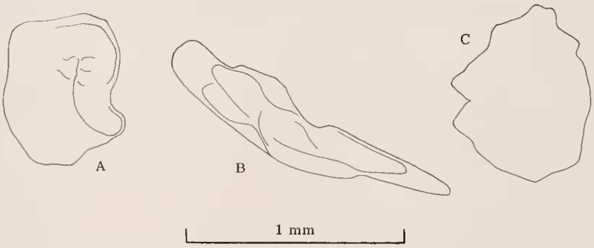

Figure 60. *Saccodon wagneri* (dental morph I), 52.0 mm. Otoliths. A. Lapillus (ventral view). B. Sagitta (lateral view). C. Asteriscus (lateral view).

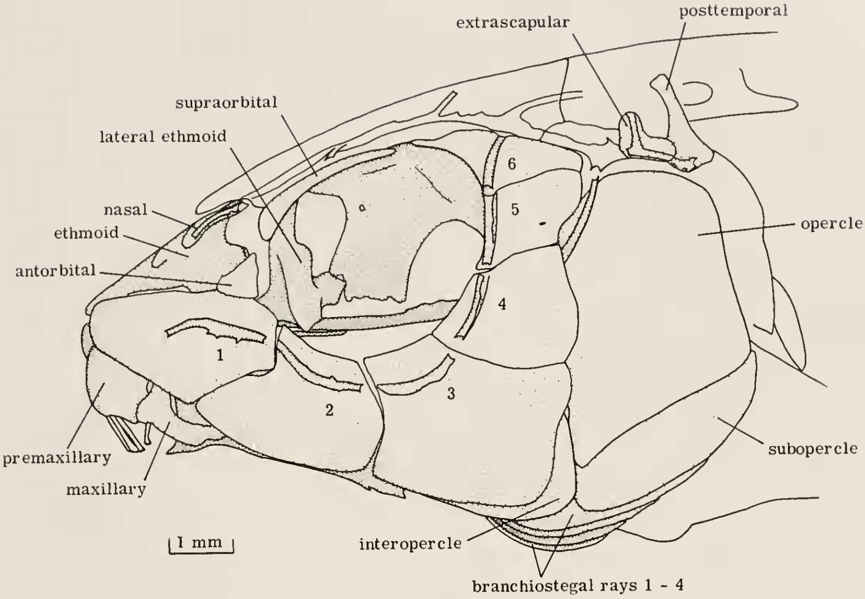

Figure 61. *Saccodon wagneri* (dental morph I), 57.2 mm. Lateral bones of skull (lateral view).

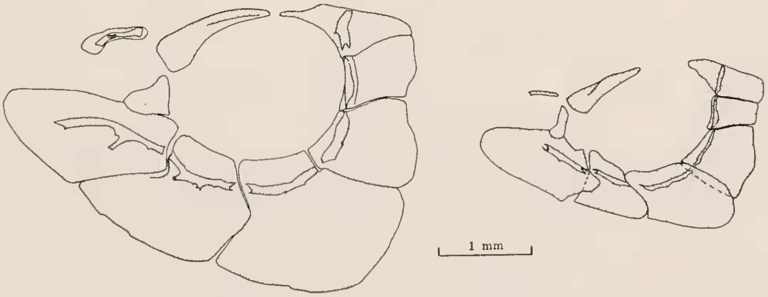

Figure 62. Parodontidae. Nasal, antorbital and circumorbital bones. Left, *Saccodon wagneri* (dental morph I), 57.2 mm. Right, *Parodon guyanensis*, 38.5 mm.

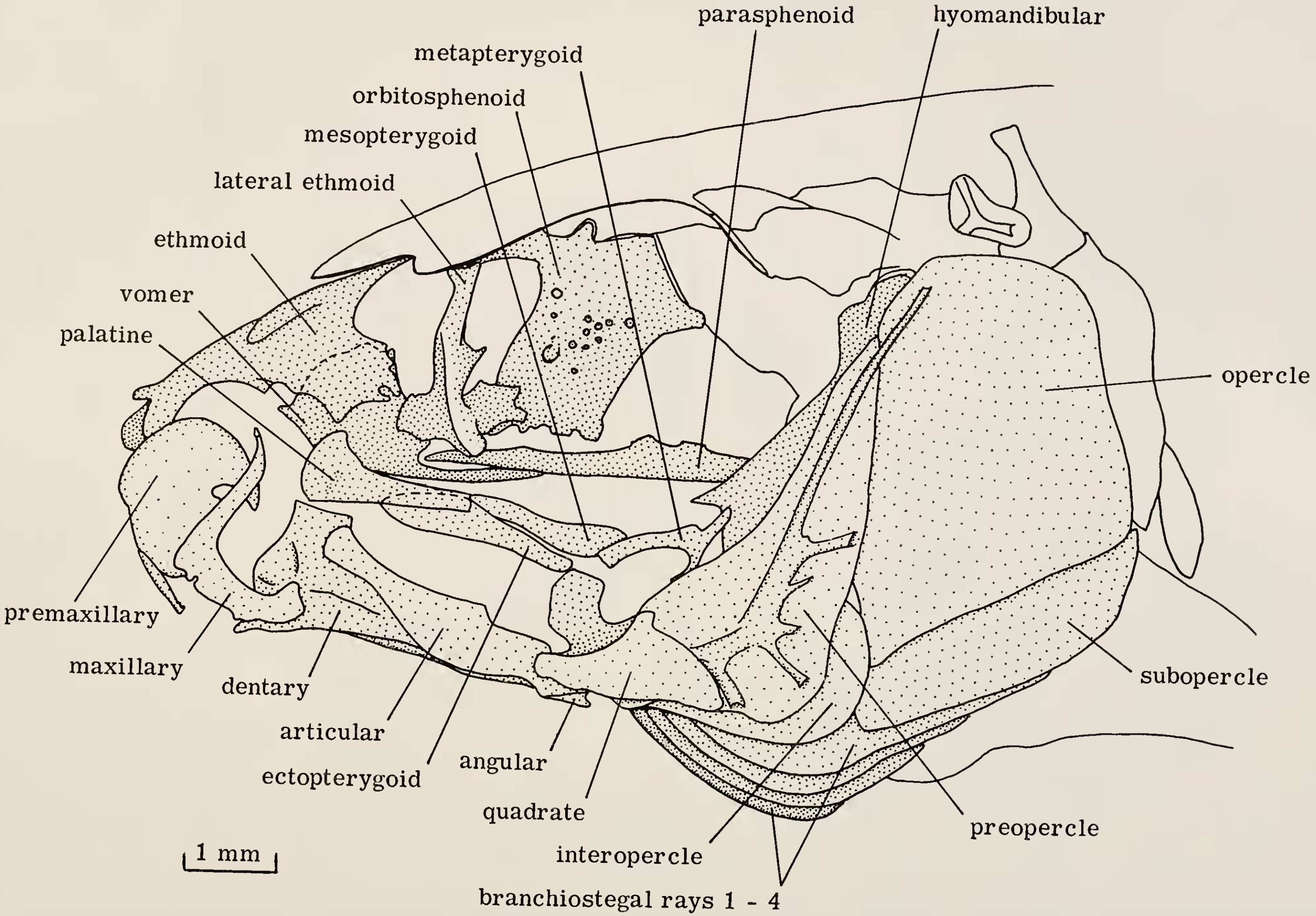

Figure 63. *Saccodon wagneri* (dental morph I), 57.2 mm. Lateral view of skull with nasal, antorbital and circumorbital bones removed.

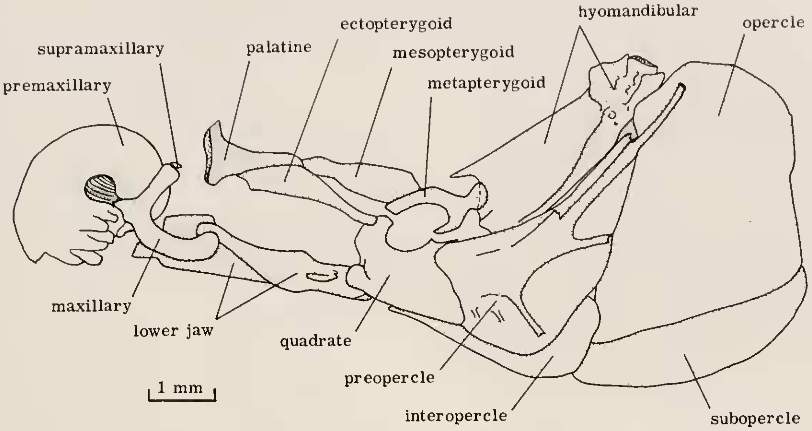

Figure 64. *Saccodon wagneri* (dental morph IV), 55.4 mm. Jaws, suspensorium and opercular bones (lateral view) (teeth removed).

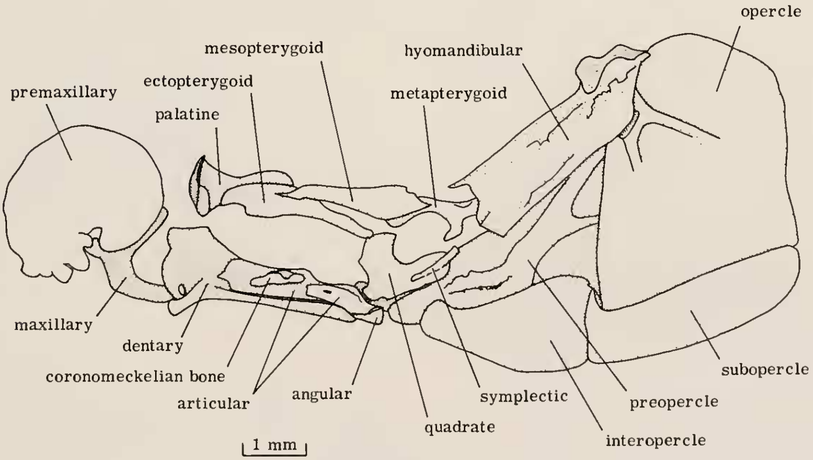

Figure 65. *Saccodon wagneri* (dental morph IV), 55.4 mm. Jaws, suspensorium and opercular bones (medial view) (teeth removed).

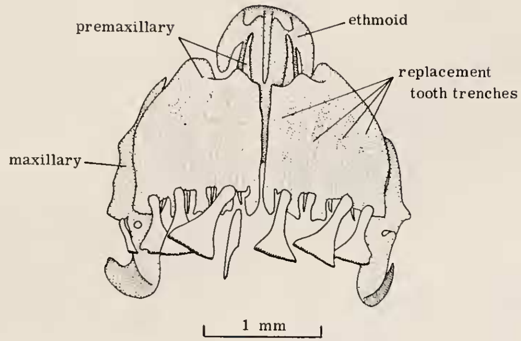

Figure 66. *Saccodon wagneri* (dental morph I), 45.5 mm. Upper jaws showing tooth replacement in progress (frontal view).

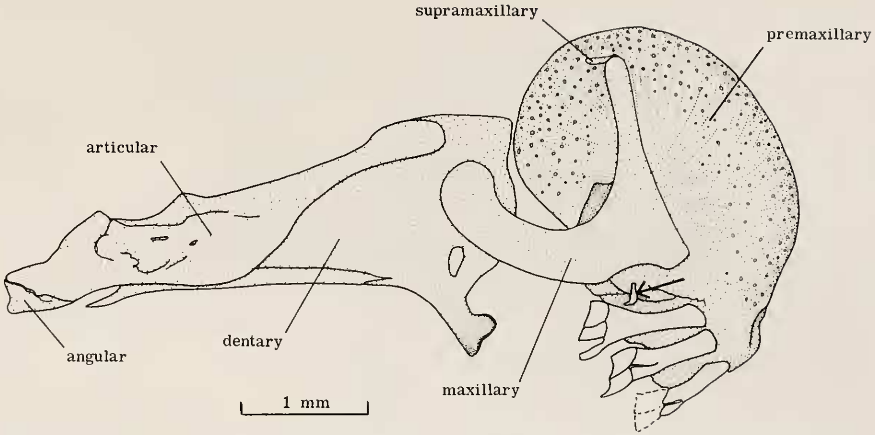

Figure 67. *Saccodon wagneri* (dental morph IV), 55.4 mm. Jaws and jaw teeth (lateral view). Note. This specimen unusual in having a minute, unicuspid, pedicellate tooth lateral to main series of functional teeth (indicated by an arrow).

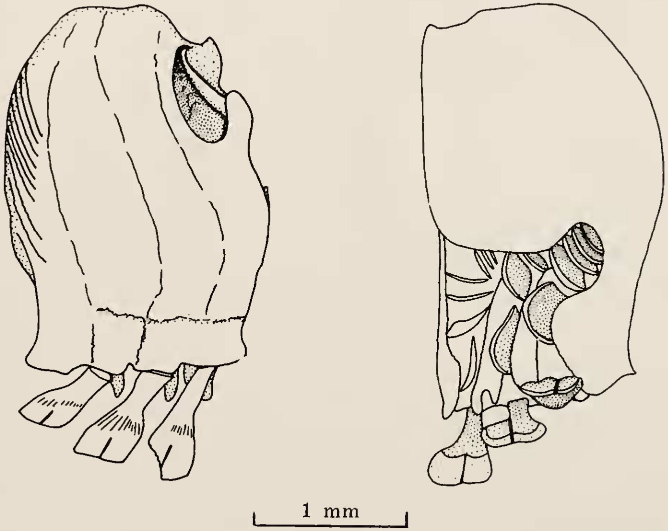

Figure 68. *Saccodon wagneri* (dental morph IV), 52.0 mm. Premaxillary bone. Left, frontal view. Right, ventral view.

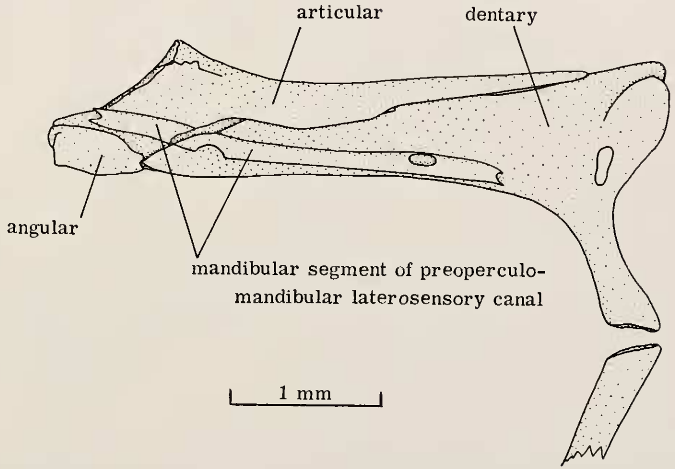
articular
dentary
angular
mandibular segment of preoperculo-mandibular laterosensory canal
1 mm

Figure 69. *Saccodon wagneri* (dental morph IV), 55.4 mm. Lower jaw (ventral view).

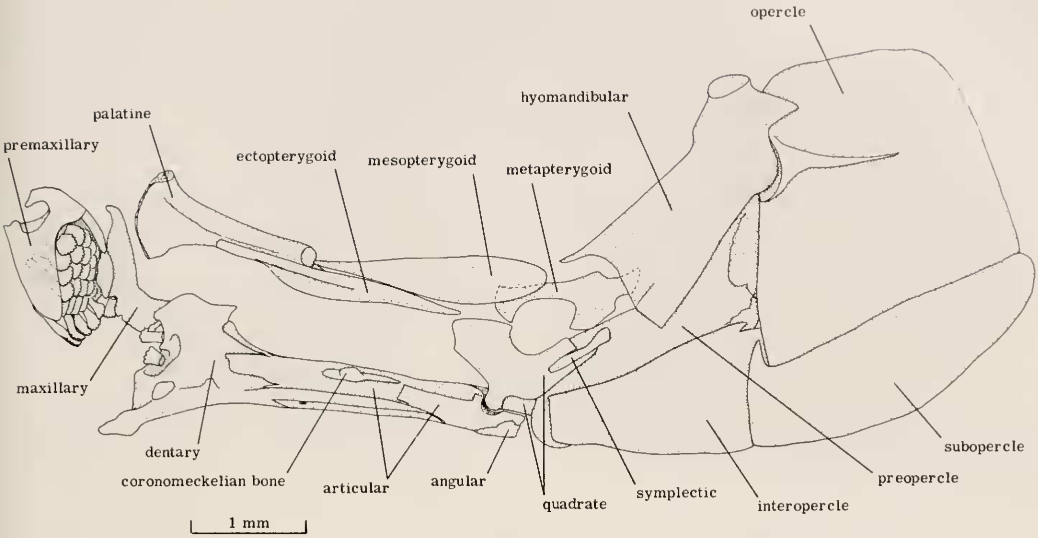

Figure 70. *Parodon guyanensis*, 38.5 mm. Jaws, suspensorium and opercular bones (medial view).

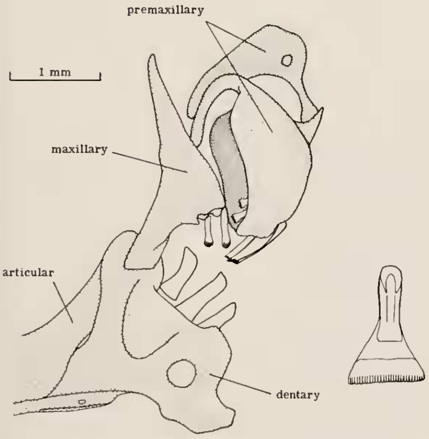

Figure 71. *Parodon caliensis*, 63.5 mm. Upper jaw and portion of lower jaw showing dentition (lateral view). Inset on right, functional tooth from premaxillary (medial view).

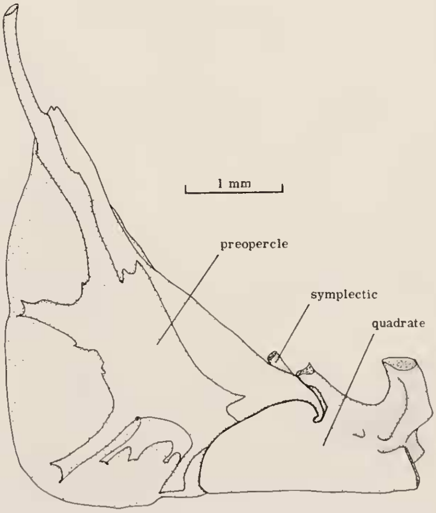

Figure 72. *Saccodon wagneri* (dental morph IV), 55.4 mm. Relation of quadrate to preopercle (lateral view).

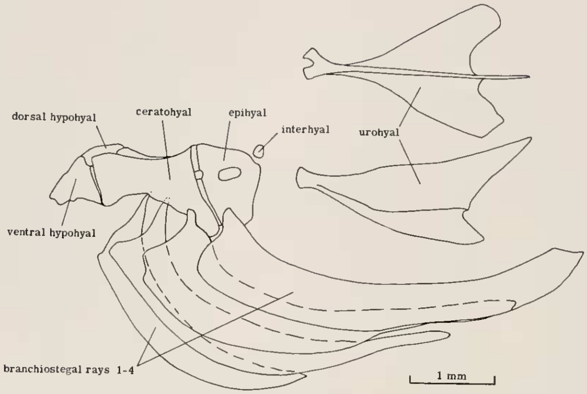

Figure 73. *Saccodon wagneri* (dental morph IV), 52.0 mm. Hyoid arch with basihyal removed (lateral view) and urohyal bone (lateral and dorsal views).

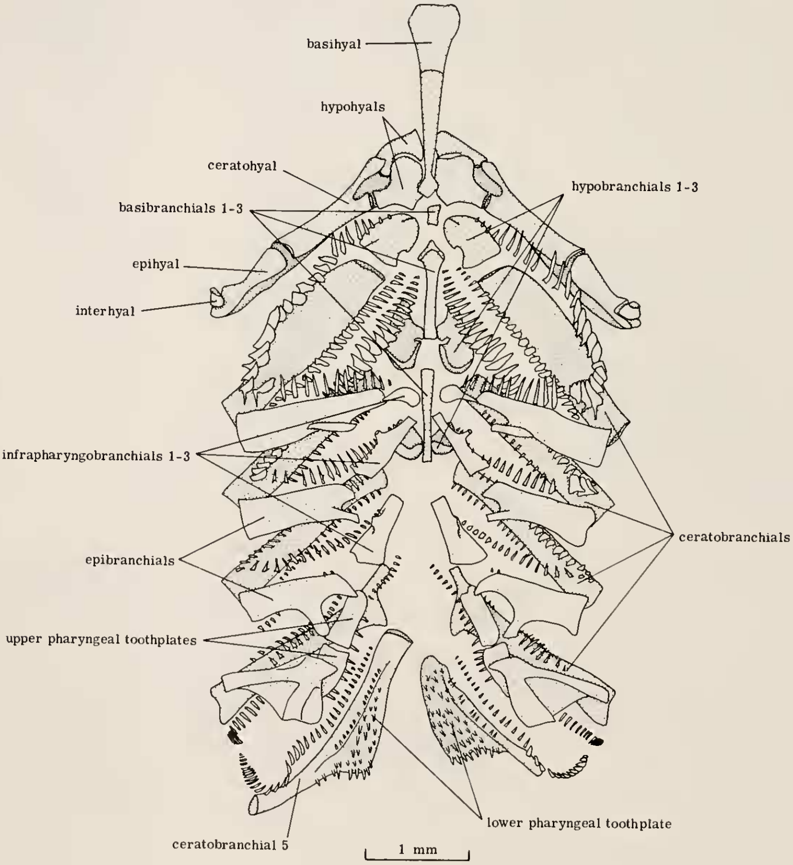

Figure 74. *Saccodon wagneri* (dental morph IV), 55.4 mm. Hyoid and branchial arches (dorsal view).

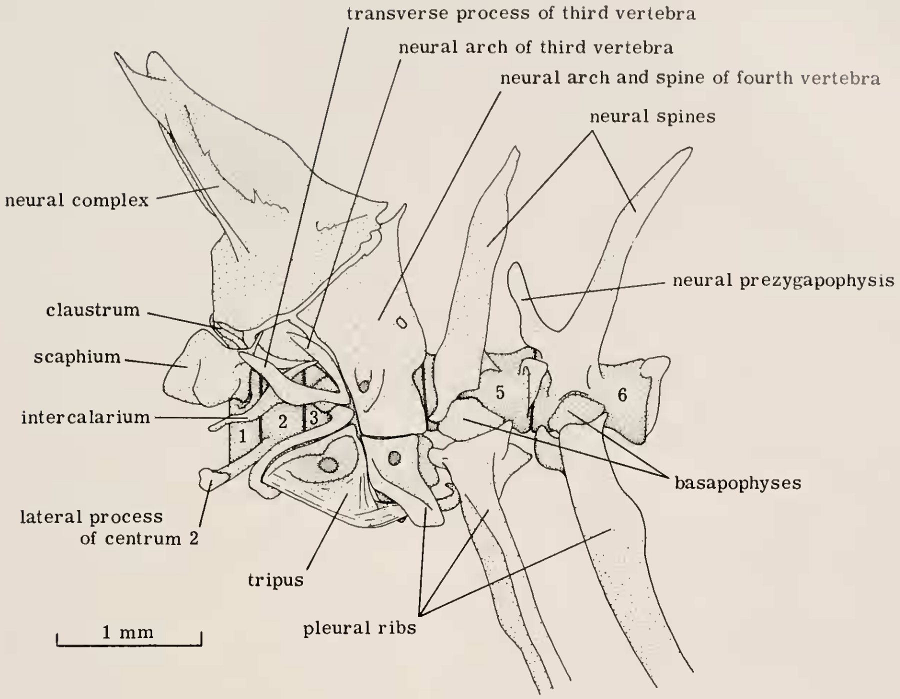
transverse process of third vertebra
neural arch of third vertebra
neural arch and spine of fourth vertebra
neural spines
neural complex
neural prezygapophysis
claustrum
scaphium
intercalarium
1
2
3
5
6
basapophyses
lateral process of centrum 2
tripus
pleural ribs
1 mm

Figure 75. *Saccodon wagneri* (dental morph IV), 55.4 mm. Weberian apparatus (lateral view).

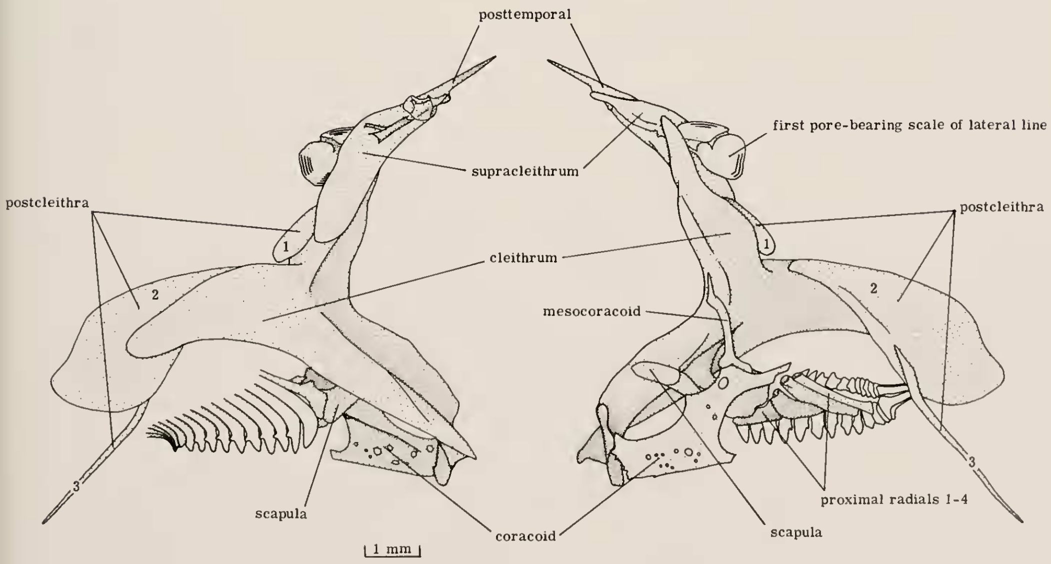

Figure 76. *Saccodon wagneri* (dental morph IV), 55.4 mm. Right half of pectoral girdle (lateral and medial views).

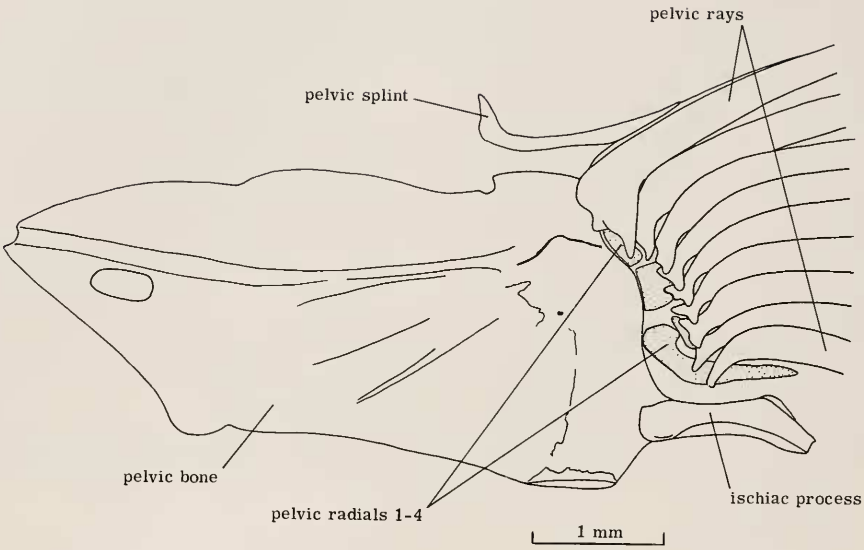

Figure 77. *Saccodon wagneri* (dental morph IV), 55.4 mm. Left half of pelvic girdle (ventral view).

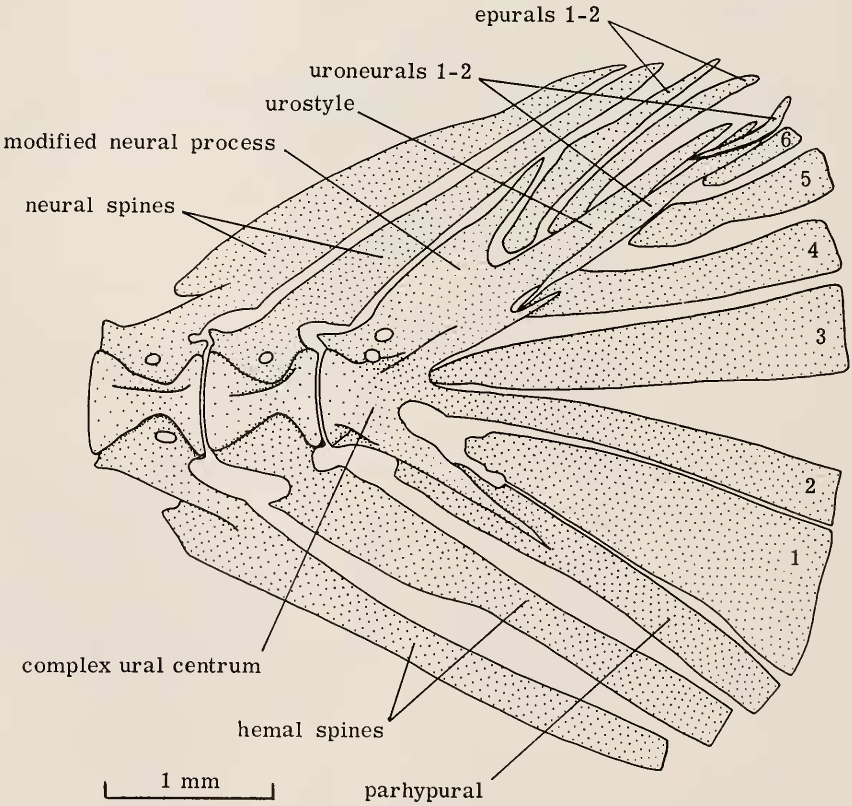

Figure 78. *Saccodon wagneri* (dental morph IV), 55.4 mm. Caudal skeleton (lateral view).